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Errata.

Page 43, 14 lines from end for "*Platyopuntia*" read "*Opuntia* (*Platyopuntia*)"
Pl. II, fig. e (following p. 19) for "*Argyroplace*" read "*Argyroploce*"
Page 336, line 13, for "*Pragmatiphila*" read "*Phragmatiphila*"
Page 629 is misprinted as "p. 626"
Page 639, line 31, for "five Protozoa" read "four Protozoa"
Page 639, line 32, for "an unidentified body" read "two unidentified bodies"
Page 662, line 5, for "Azores : Madeira" read "Azores. Madeira."
Page 669, line 6, for "Allotype ♂" read "Allotype ♀"
Page 701, line 1 of Summary, for "all of which" read "all but two of which"
Page 713, 3 lines from end, for "Sinton (1933b)" read "Sinton (1933c)"

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

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OBSERVATIONS ON COLLECTING PARASITES OF *CACOECIA HISTRIONANA* (FROEL.) (LEP., TORTRICIDAE).

(PLATES I–III.)

By Jost M. FRANZ.
Commonwealth Institute of Biological Control.

Cacoecia histrionana (Froel.) is a European species similar to the spruce budworm, *Choristoneura fumiferana* (Clem.), of North America. Although it has been recorded in central Europe from all natural and many cultivated spruce forests between the Carpathian Mountains and southern France, no outbreak has ever been reported. It was hoped, therefore, that beneficial parasites responsible for holding the insect in check might be found which could be used in Canada to control the spruce budworm. After the situation had been reviewed by J. J. de Gryse in 1946, W. F. Sellers and G. E. Bucher were sent to Europe by the Commonwealth Institute of Biological Control in 1947. Mr. Sellers returned to America about the middle of 1947 and the investigations were continued by Dr. G. E. Bucher and his assistants, including H. Eidmann, F. Groschke, and the writer. The first infestation was located by Groschke but owing to the scarcity of the species, no large-scale collecting could be made. During 1949 the writer was asked to ship as many parasites of *C. histrionana* as possible to the Dominion Parasite Laboratory at Belleville. This paper is a report of the work carried out in Europe (Germany) during 1948 and 1949 in order to provide some preliminary information on the host and its parasites in the field. It is hoped that it will facilitate the rearing and liberation of the budworm parasites and indicate the possibility of natural control of the Canadian spruce budworm, by the insect parasites of its European relative. This study was conducted under the supervision of L. P. Mesnil, in charge of the European Laboratory of the Commonwealth Institute of Biological Control at Feldmeilen, Zürich. The photographs shown on the Plates are by the author.

Areas of Infestation.

(*a*) *Survey*. Eidmann's (1949 a, b) review of the areas in which *C. histrionana* is known to have occurred covers the past 110 years. It was necessary, however, before the collection of parasites on a large-scale could be planned, to obtain some more details about the actual incidence of the species. Therefore, starting from Hohenthan, eastern Tirschenreuth, north-eastern Bavaria, where the moth had been located most recently, the area near the eastern frontier of Bavaria southwards to Zwiesel was scouted for caterpillars between 20th May and 1st June 1949.

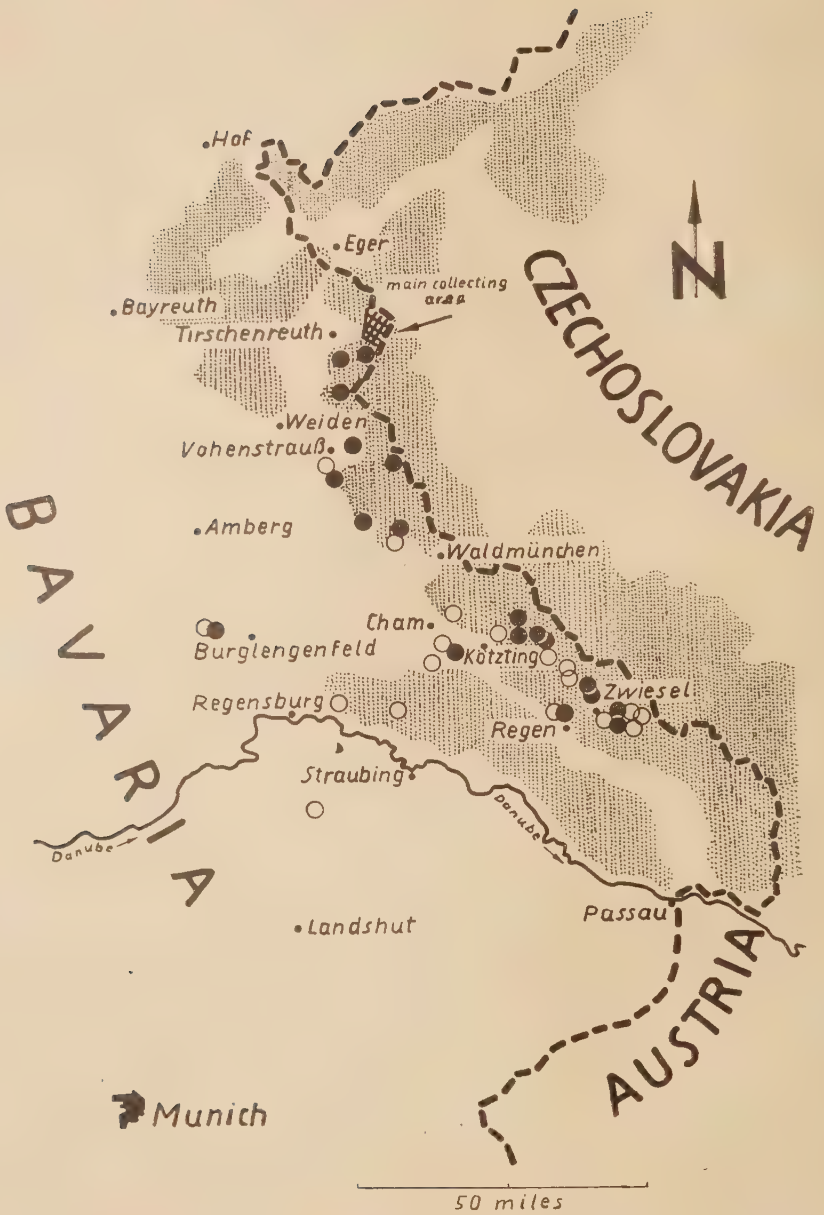
Hof
Eger
main collecting area
Bayreuth
Tirschenreuth
Weiden
Vohenstrauß
Amberg
Waldmünchen
Cham
Burglengenfeld
Kötzting
Zwiesel
Regensburg
Regen
Straubing
Danube
Danube
Passau
Landshut
Munich
BAVARIA
CZECHOSLOVAKIA
AUSTRIA
N
50 miles

Fig. 1.—Distribution of *Cacoecia histrionana* obtained from samplings collected at the end of May, 1949.

The results are shown in fig. 1 ; black dots indicate where at least one larva was found and empty circles where no larvae were collected. Because of the great difficulty in finding the caterpillars in their webs, at least half an hour per person was spent at each spot. Spruce stands along the edges of 20- to 50-year-old forests were chosen for the most part, since, according to present knowledge, they are favourable to *C. histrionana*. With the exception of the most westerly point investigated north-west of Regensburg (350 m.), these areas were at elevations of 500 to 800 m. It may be noted that no infestations were located in the southern part of the Bavarian Forest, although four places were thoroughly examined. This does not prove, however, that it does not exist there. During the summer of 1949 the species occurred in ecologically suitable areas everywhere in the Upper Palatinate and the eastern Bavarian Forest. Also its regular occurrence outside the scouted areas is very probable, for instance in the Czechoslovakian part of the forests and in the Fichtelgebirge. Apart from the main collecting area east of Tirschenreuth, the greatest number of larvae per time unit was found east of Vohenstrauss and north of Zwiesel.

The climate of the infested area examined is for the most part comparatively cool and rainy. Neither cool temperatures nor heavy precipitation seem to be necessary for the Tortricid, although they are required by the spruce. This is concluded from the occurrence of *C. histrionana* north-west of Regensburg where there is a much warmer and drier climate and pines predominate. The same may also be inferred from the distribution map of Eidmann (1949b), since their distribution extends far west of the natural spruce area to 2° E. longitude in southern France. The possibility of concluding from these observations that the optimum climatic conditions for the species occur outside its local living range will be discussed later.

(*b*) *Main collecting area.* The search for new haunts in the vicinity of Tirschenreuth was not resumed until 5th June owing to the lack of satisfactory collecting places previously found. The result of the search was the finding of the "main collecting area" to the east, surrounding the village of Grosskonreuth. The collecting points ranged mostly from an altitude of 600 to 750 m. at the edges of 20- to 50-year-old plantations. The search centred near the "Althergotts-Kapelle" in the north, on the western slope of the Poppenreuther Berg in the east, and near Hermannsreuth in the south of Grosskonreuth.

TABLE I.

Climatic conditions at the main collecting area east of Tirschenreuth, 650 m. above sea level. 1949.

Month	Air temperature °C.		Amount of precipitation		Summer days*	Frost days†
	Average of month	Deviation from norm.	mm. per month	Percentage of norm.		
Jan. ...	−2·1	+1·3	32	56	—	25
Feb. ...	−1·4	+0·9	22	50	—	24
March ...	−0·8	−1·7	60	110	—	25
April ...	7·8	+2·9	46	76	—	9
May ...	10·2	0·0	140	207	1	4
June ...	11·7	−1·7	78	93	2	1
July ...	15·4	+0·4	22	22	8	—
Aug. ...	15·1	+1·1	53	61	12	1
Sept. ...	13·6	+2·8	26	44	4	2
Oct. ...	8·2	+2·3	15	27	—	9
Nov. ...	1·2	0·0	28	52	—	21
Dec. ...	0·6	+2·0	79	113	—	19

†Minimum temperature below 0°C. *Maximum temperature above 25°C.

Table I shows the actual climatic conditions in 1949, and their deviation from the normal. It appears that this year had approximately average temperatures being a little warmer only during the autumn. All months except March, May and December had less precipitation than the average. It is remarkable that July was the only month without at least one day with frost The average temperature of the year is 5 to 6°C., and of the vegetative period (April to, and including, August) 12 to 13°C. The average number of days with frost in this locality varies between 135 and 150, the average amount of precipitation being 800 to 900 mm. On 190 to 200 days the air temperature normally exceeds 5°C., on 130 to 190 days 10°C. Only the lower levels are used for agriculture ; the photographs (Pl. I, *a*, *b*) show the type of landscape and spruce forests.

Life-history.

The life-history of the budworm may be summarised as follows. The scale-shaped eggs, similar to those of the North American spruce budworm, are laid in double rows on the needles of spruce ; they usually hatch in about two weeks. The young larvae begin to mine single spruce needles and continue to feed, first in this way and later by nibbling the needles from the outer edge, until they are forced to pause by the autumnal drop in temperature. There is no diapause and the larvae resume feeding when the temperature rises. The majority of the young larvae hibernate during the first half of their development ; they feed upon old needles during the autumn, but prefer new shoots during the spring and summer and move only inside a funnel-shaped web which is extended up to the feeding places. There are ten larval instars, according to Eidmann (*l.c.*). Pupation occurs at the feeding place or at more sheltered points in the crown. After two to three weeks the moths emerge, mostly in the months of July and August. The males display a characteristic zigzag pairing flight on warm evenings at sunset, while the females wait in the crowns. These facts, in part already discovered by other authors (Eidmann 1949b, Groschke 1949, Wachtl 1882), are supplemented in some respects. Unless otherwise noted all observations were made in the main collecting area.

Breeding Places. *C. histrionana* larvae are mainly to be found on the edges of 20- to 50-year-old spruce woods. Here the dense strata of overlapping branches seem to favour the simultaneous striving of the caterpillars for food and cover. Occasionally, they were also found on much younger (only 1·5 m. high) or on old trees. No preference for any particular sheltered position or quarter was noted and the distribution throughout a crown was fairly even, as shown by examination of felled trees. The caterpillars and their main parasite were also found in a small isolated plantation 1,400 m. away from the nearest forest (Pl. I, *c*).

Webs. About half of the larval webs were in new shoots in May, and 70 to 80 per cent. at the end of June. The hiding place, to which the larvae retired if disturbed, was often some centimetres distant from the feeding place (Pl. II, *a*). Occasionally, they will hide in an abandoned web of *Epiblema tedella* (Cl.) or a dried gall of *Chermes abietis* L. Some of the webs in which pupation takes place (Pl. II, *b*) were found far distant from feeding places, for example on finger-thick branches and in the middle of the crown. Whether or not pupation takes place on the ground remains uncertain, but it is considered very improbable.

Development. The main characteristic of the development is the great variation in the stages to be found at any given time. There are caterpillars at every season. The late larvae of one generation are still present in the field when the majority of the larvae of the following generation are already hatching. On 20th and 21st May 1949 several full grown larvae and the first prepupa were found, and the first pupa on 5th June. On the other hand, quite small larvae were discovered (head capsule 0·55 mm.=instar 5*) on 17th June, one of about the same size on 25th June, one (head capsule 0·94 mm.=instar 7) on 25th June, and several others that could not be measured. Neither the percentage of parasitism nor the mortality of the small larvae found in June and July deviated from the average.

There is usually one generation a year which passes the winter as a larva. Whether or not, in the case of eggs laid early in the year, moths may occasionally be produced in the same year cannot be positively concluded from the facts at hand. The majority

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*All calculations of instars are based on the measurements of ten instars given by Eidmann (*l.c.*). Recent observations of GROSCHKE indicate that the average number of eight larval instars may vary according to the conditions of the rearings. The problem needs further study.

of the larvae (approximately 60 to 70 per cent.) in this area pupated between the middle and the end of July. The adults emerged two to three weeks later.

Overlapping of the stages in development is caused by two factors. Firstly, the microclimatic conditions acting upon the larvae during their long development vary considerably, the environmental conditions differing greatly according to whether the larvae are located on the sunny or shady side, southern or northern edge of the stand, etc. Secondly, there is some variation in the duration of development, apparently due to intrinsic differences. In the spring of 1949, 1,800 larvae were collected and reared under similar conditions. The great majority pupated normally but there were some stragglers that did not pupate until December and even then a few had failed to pupate. This group, with a prolonged developmental period, is estimated to have been between 1 and 2 per cent. It is possible that they suffered from a pathological disability to produce enough hormone for pupation. This view was supported by Dr. O. Pflugfelder, Hohenheim, who kindly studied some of the non-pupating larvae. According to F. Groschke (verbal communication) larvae reared from *one* egg cluster in the same cage, did not develop at a uniform rate, four emerged as adults while the majority were still in the larval stage. The consequences of this variation in developmental velocity caused by external and internal factors will be dealt with later.

Hibernation. The hibernation webs of the younger larvae are difficult to find owing to their small size. Usually there is a tube-like web connecting the mined or, in the case of older larvae, the externally damaged needles (Pl. II. *c*). A branch of the web tunnel often leads under a bud scale or as a last resort into an old web of *E. tedella.*

To determine the distribution of the hibernating larvae, of which very little is known, a small isolated plantation was selected (Pl. I, *c*) in which the initial *Cacoecia* population was small and in which 400 pupae had been introduced in the middle of July. On the 16th and 17th October 1949, two trees about 25 years old were thoroughly searched. Each twig had to be examined all over with a lens and it was discovered that all levels of the crown were more or less evenly populated but some preference was shown for the inside. The variation in the rate of larval development, previously mentioned, was again evident ; of 52 larvae found *in situ*, one was full grown (head capsule 1·61 mm.=instar 10), two about instar 8 and 9, eight about instar 6 and the remaining 41 between instar 3 and 5. This inequality is all the more surprising in view of the stabilising effect one would have expected from the simultaneous introduction of 400 pupae only three months previously.

The lower temperature limit of activity. Temperature limits the duration of feeding in the autumn and its initiation in spring. This lower temperature limit was determined by two somewhat primitive methods which, however, may be sufficient to give an approximate figure. Thirty-five test larvae were collected in the field in

TABLE II.

Feeding activity of young larvae of *C. histrionana.*

Temperature °C.	0·0–0·9	1·0–1·9	2·0–2·9	3·0–3·9	9·0–9·9
Frass ... ... Pellets per 24 hours ...	3·5 0·3 1·0	4·3	10·5 8·7	15·0 10·0 12·5 13·0 11·5	400 404
Mean	1·6	4·3	9·6	12·4	402

Although a complete range of temperatures was not available, it can be seen that the feeding activity almost ceases below 3°–4°C.

October and kept in the laboratory at 0 to 5°C., *i.e.*, under natural conditions (for the feeding test 26, for the locomotor test 9 larvae). The activity of feeding was measured by counting the frass pellets dropped per time unit at different temperatures. The results are given in Table II.

Locomotor activity was examined by a method (Franz, 1940–41) based on positive phototaxis, in which the larvae were forced to crawl in a glass tube equipped with a thermometer. At 1° and 2°C. all larvae turned to the light, but very few were able to crawl. Only when the temperature reached 3° and 4°C. could the larvae move a short distance, up to 8 cm. during one test of six minutes. The instars corresponded to those found in the field (instars 3 to 8). No differences were observed in the position of the zero point of the various instars. Even the velocity of movements was about the same when plotted against the length of the larvae.

The results of both these tests are, therefore, approximately the same ; that at temperatures exceeding 3 to 4°C, the larvae become active and crawl towards food. In this connection it may be mentioned that the annual number of days on which the average temperature exceeds 5°C. ranges from 180 to 210 in the area where the species was found in 1949 (fig. 1). It must, however, not be overlooked that the decisive factor is the body temperature of the larva, which is influenced strongly by radiant heat. Furthermore, the possible bearing of the gradient of evaporation is totally neglected in this preliminary observation (*cf.* Wellington, 1949). The zero point for locomotor activity of 7°C., given by Eidmann (1949b), is probably to be attributed to the fact that he was not able to use larvae collected from natural hibernating places for his tests.

Flight period of moths. This was prolonged in a manner corresponding to the variation in the duration of development observed in the larvae. According to Eidmann (*l.c.*) moths have been caught from the end of May to the beginning of September. A further extension of the flight period is improbable because the males only fly on warm evenings. For instance, on 21st August 1949, no moths were observed on the wing at 12 to 13°C. air temperature although enough adults had emerged but, at the same place five days later, plenty were flying at 19 to 20°C.

Theoretically, without diapause and taking into consideration the effect of the wide climatic differences of the various habitats of the larvae during their long development, the process might become completely irregular. The dependence of flight on temperature and, perhaps also a higher mortality of older overwintering larvae and pupae, are thought to be the most important factors causing a limited synchronisation of development. The epidemiological consequences of this incomplete synchronisation are referred to later.

Population Density and Collecting Methods.

After the discouraging experiences of the preceding years, it was considered that the species might prove to be extremely rare. During preparations for the large-scale collecting mentioned above, it was discovered that the Tortricid occurred so regularly in certain areas that it could be collected by untrained workers. The main collecting area proved particularly favourable for the purpose because of the abundance of middle-aged and multi-edged spruce forests.

For a quantitative measurement of population density, the larval stage is particularly suitable because only this stage lives long enough and can be found under nearly all weather conditions. The adults are hardly ever seen during the day and are difficult to flush ; in the evening they swarm in favourable weather for a short period only and in a manner that makes counting very difficult.

In order to assess the density of population approximately at three good collecting places, samples were taken very carefully over a known length of forest edge. These sampling lines were examined twice in order to reduce any error caused by larvae having been overlooked. In spite of this, the numbers quoted below can only be

TABLE III.

Population density of larvae of *Cacoecia histrionana.*

Locality	Metres searched	Proportion of crown searched	First search			Second search			Ratio of first to second search
			June 1949	Number of larvae	Larvae per metre	July 1949	Number of larvae	Larvae per metre	
1. North of Baernau	30	$\frac{1}{6}$	27th	21	0·70	19th	7	0·23	3·0 : 1
2. North of Baernau	600	$\frac{1}{5}$	19th	91	0·15	–	–	–	–
3. Poppenreuther Berg... ...	1,200*	$\frac{1}{5}$	22nd	202	0·17	20th	29	0·058	2·9 : 1

*Second search only 500 m.

regarded as minimum values. Collecting and counting was carried out at edges of forests only, at heights ranging from 0 to 2 m. (Pl. I, *d*).

The following conclusions may be drawn from Table III. Firstly, twigs which have been searched and from which the larvae have been removed are repopulated within four weeks, probably by movement within the crown concerned. At the end of this period, a number of larvae about equal to one-third of the original population could be found (Table III, nos. 1 and 3), irrespective of the size of the population. Secondly, since the distribution of larvae over the crown was fairly even, as several samples showed, the minimum size of the population of the sampling lines at this time can be calculated by relating the proportion of the crown searched to the total. The results are as follows : No. 2, 455 larvae in a distance of 600 m. examined (=0·74 larvae per m.) ; No. 3, 1,010 larvae in 1,200 m. (=0·84 larvae per m.).

A somewhat rough calculation might be made of the total number of larvae living in a larger region, by means of the data mentioned above. The western part of the Poppenreuther Berg seems to be suitable for this, because most of the collections were made there. The forest edges searched were divided into three density categories ; for the first, the density of larvae was found to be about 0·84 per m. (No. 3), for the second, half as much and for the third, a third as much was estimated. Of the 14,000 m. of the suitable edges of the forest at the west side of Poppenreuther Berg (covering some 750 acres at an elevation of 600 to 750 m.) 9,000 m. were searched ; 2,000 m. belonged to the first category and 3,500 m. each to the second and third. From this, the larval population at the edges searched may be calculated to be between 4,000 and 4,500. For the parts not examined, a density of larvae somewhere between the second and third categories was assessed, which in all makes a population of about 6,000 larvae for the suitable forest edges. Since some larvae also live inside the forests, even if they are not so numerous as on the edges, probably an equal number might be estimated for the whole interior of the forest. The result of these calculations is a total of at least 12,000 larvae (=16 per acre) for the west side of Poppenreuther Berg in June 1949.

This number, of course, is a very rough estimate, being based on only a few counts and many assessments. After spending more than 40 days searching in the area concerned, the writer is of the opinion that the figure of 12,000 is most likely to be an underestimate than the reverse. For the whole region of the main collecting area, there must certainly have been more than 100,000 larvae in June 1949. Thus *C. histrionana* is not an excessively rare species. This conclusion agrees with notes supplied by Groschke (*l.c.*) who was able to collect a good many moths south of the main collecting area during 1947 and 1948. On the other hand, the numbers are very small compared with population densities, even in the initial stages, of mass outbreaks of other forest insects. The absence of mass outbreaks, mentioned several times by Eidmann (*l.c.*), will be dealt with later.

Something may be said here of the sampling methods. Because it was difficult for untrained collectors to find the right species of larvae, the collectors (men and women) were not paid at a piece rate, but per hour as is usual with forest workers. The wages were increased by an additional reward for each larva exceeding 10 per day and by a further reward for the best total for the day. The caterpillars were picked by hand which entailed considerable practice and the results showed remarkable improvement as time went on. The six workers, mostly girls, averaged 2·02 larvae per hour for the first 12 days. This seems to be about the lowest limit of abundance at which unskilled labour can be satisfactorily used, for the interest of the collectors falls off quickly if the results are less. In the following 10 days each collector averaged 4·0 larvae per hour, the best 4·9, the worst 3·3. The best result reached was 55 larvae in eight hours (6·9 larvae per hour). The results of the individual days showed that, in spite of all differences in the frequency in single cases, the average results and therefore the average larval density fluctuated very little.

NATURAL ENEMIES.

The Species of Parasitic Hymenoptera.

It was of importance in connection with the present problem to learn whether or not parasites cause an appreciable mortality of *C. histrionana* and if so what species are concerned. In order to give reliable values in conventional terms of percentage parasitism, observations must be based on a large number of collections gathered at all stages of the host and made over a long period of time at various localities. Moreover, many dissections of the host should be made so as to avoid additional errors caused by mortality during the period of rearing.

These demands could not be met because most of the time had to be devoted to collecting ; this was the drawback of working on a host species of which, at best, four specimens per hour were to be found. In view of these qualifying reservations the figures and percentages of parasitism as presented here can only be taken as an approximate guide to the real status and minimum effect of the parasites in the field.

The parasites reared from *C. histrionana* in the summer of 1949 are listed Table IV. In the case of each species an indication is given as to whether it is a primary parasite (P), a hyperparasite (H), whether the larvae or pupae of the host were attacked and how many specimens were reared. The number mentioned for *Meteorus ruficeps* may not be exact because 542 specimens were shipped to Belleville before hatching, and could not be identified except by the cocoon. Judging by the samples retained and the scarcity of all the other species of parasites the error, if any, is not believed to exceed 1 per cent. Table IV lists 16 certain and doubtful primary parasites and three—four if *Amblymerus subfumatus* is included—hyperparasites. A small sample of 75 host larvae collected by Groschke and the writer in the neighbouring area to the south in 1948 had yielded the following species : *Ephialtes pictipes* (2), *Angitia rufipes* (2), *Apanteles dilectus* (1), *Apanteles ater* (1), *Meteorus ruficeps* (12). All these species except *Apanteles ater* were also reared in 1949. The prevalence of *M. ruficeps* in both years may be noted.*

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*Wagner (1929) lists *Angitia claripennis* Thoms. and *Glypta flavolineata* Grav. as reared from *C. histrionana* in Germany. Except for the date of hatching, 15th and 16th June, no further details are given. The identification of the Ichneumonids by Brauns may be somewhat doubtful.

TABLE IV.

List of Parasitic Hymenoptera* bred from *Cacoecia histrionana*† in 1949.

Species	Status	Stage of host attacked	Number of parasites reared
Ichneumonidae.			
Phaeogenes ?semivulpinus (Grav.)	P	Pupa	1
Hemiteles areator (Panz.)	H?	Larva and pupa	2
Pimpla turionellae (L.)	P	Larva (and pupa ?)	2
Apechthis resinator (Thunb.)	P	Pupa	3
Ephialtes pictipes (Grav.)	P	Larva	4
Lissonota sp.	P	Larva	1
Omorgus mutabilis (Hlmgr.)	P	Larva ?	1
Angitia rufipes (Grav.)	P	Larva	6
Angitia sp.	P ?	Larva	1
Mesochorus ?orbitalis Hlmgr.	H	? (Host : *M. ruficeps*)	5
Tryphoninae, gen. ?	P	Larva	1
Pezomachus sp. ‡	H	Pupa	1
Braconidae.			
Apanteles dilectus (Hal.)	P	Larva	3
Apanteles xanthostigma (Hal.)	P	Larva	1
Microdus dimidiator (Nees)	P	Larva	2
Meteorus ruficeps (Nees)	P	Larva	613§
Pteromalidae.			
Amblymerus subfumatus (Ratz.)	P and H	Pupa : *C. histrionana* Cocoon : *M. ruficeps*	14 (ex 5 hosts)
Eulophidae.			
Elachertus dimidiatus (Nees)	P	Larva	1
Tetrastichus evanescens (Ratz.)	P ?	Larva	1
Unknown species, mostly cocoons which did not emerge			14

*Identified by Dr. C. Ferrière of Geneva.

†Number of host larvae and pupae, 1,712. In addition 250 host larvae were sent to Belleville before the parasites emerged.

‡Caught when attacking host pupa.

§Only approximate number ; see text.

Parasites as Mortality Factors.

Owing to the prolonged larval development of *C. histrionana* the parasitism of the larvae was expected to increase between hibernation and pupation In such instances several samples are usually collected during the development of the hosts in order to discover when the various parasite species attack them It should be stressed that the real value of parasitism cannot be obtained by plotting the number of parasites hatched from the samples successively collected, against the total number of host larvae collected. This error occurs quite frequently in the literature. On the contrary, in the case of parasites remaining inside the host up to its last instar, only the last sample before pupation gives the minimum value of the effect of the parasitism of the larvae, and in the same way the last sample before adult emergence gives the minimum value of the effect of the parasitism of the pupae ; insects collected and caged at an earlier date are removed from any possible subsequent attack. The real value of the quantitative effect of the parasitism can only be assessed when data has been obtained on the effect of attacks on the sample rearing ; these attacks may be the direct cause of mortality or they may result in diseases being transferred from one host to another by the parasite. If some parasites leave the hosts before a certain stage is completed, such as the egg, larva or pupa, and if traces of their existence are not to be found within the last sample, the percentage of parasitism of earlier samples should be combined with that of the last sample.

In view of these considerations, the larvae of the Tortricid were collected at three different periods (Table V). In the first period overwintering larvae were taken and in the other two, in the summer, larvae in various stages of development. As the only parasite, *Meteorus ruficeps*, found hitherto in hibernating larvae, emerged at the beginning of June, the reduction in host population due to early parasitism had to be taken into account in calculating the degree of late parasitism in order to find the minimum value of larval mortality caused by parasites. The percentage of parasitism found at the second search did not have to be considered separately because *M. ruficeps* only hatched shortly before and during the third collecting period; empty parasite cocoons remained for some time in the larval web, indicating that the parasite had already emerged from the host. Thus, at the third search, apart from the parasites that had overwintered in the hosts, most of the effect of summer larval parasitism could be determined. The timing of the collections as explained above could be applied to the bulk of the population only and thus a considerable part, about a third, might not have been taken at the optimum moment (compare p. 5). Using this method which requires a very thorough search, the rates of parasitism are more likely to be under- than over-estimated. It may be that the relative insignificance of parasites other than *M. ruficeps* is partly due to the fact that most of the caterpillars were collected in June, perhaps before the main flight of the other species occurred. Under the circumstances given, however, the method applied probably yielded the best results obtainable.

Parasitism of the pupae could be determined only very approximately because very few pupae were to be found after the elimination of so many larvae by parasites.

Parasitism of Larvae.

Table V shows that the percentage of parasitism increases during the course of the summer independently of the decrease in the number of larvae after pupation begins. The first sample was taken about 10 km. south of the main collecting area and at the same altitude. The degree of parasitism was calculated as a percentage of the total number of living and dead host larvae, pupae, and adults which were taken from the cages after rearing was finished, in addition to those taken in the field. The total was about 10 per cent. less than the original number of larvae put in to the cages, as some were able to escape and slight cannibalism was brought about by crowding. A larval mortality in the cages of about 20 per cent., not attributable to parasites, was probably caused by rearing conditions falling short of the optimum. The results of rearings from the last collection include those where parasitised cocoons were found in the field during collecting as mentioned above. It is assumed in the present study that mortality in the cages was the same for parasitised and unparasitised larvae.

The rate of parasitism of about 50 per cent. found by Groschke in 1948 in approximately 75 larvae collected mostly at the beginning of July 1948 agrees well with the above results shown in Table V. The most interesting fact was the predominance, in both years, of one species, *M. ruficeps*; it was still evident in the sample III of July 1949 although only approximate figures can be given.* This predominance is attributed to the ability of the parasite to complete two or three

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*A further mass collection of *C. histrionana* was made in the same area in 1950. From 868 larvae and pupae collected between 27th June and 12th July, 431 cocoons of *M. ruficeps* (49·6 per cent. of the actual local population) were obtained. This result, based on collections made in the same period between sample II and III of 1949, confirms also the observations of the previous year. No special attention could be given on this occasion to hatched cocoons in the field and to other parasites.

TABLE V.

The seasonal increase of parasitism of larvae of *C. histrionana*.

	Date of collection, 1949		
	18–22 May Sample I	15–28 June Sample II	19–27 July Sample III
Host Larvae.			
(*a*) Living, either reared or found in the field beside parasite cocoon	44	1,416	215
(*b*) Dead, either reared or their webs found in the field beside parasite cocoon	—	—	63
Host Pupae.			
(*a*) Unhatched	—	5	37
(*b*) Hatched	—	—	23
Total host population	44	1,421	338
Parasites.			
(*a*) Reared and unhatched cocoons collected in the field ... ... (in brackets cocoons of *M. ruficeps*)	3 (3)	499 (478)	155 (about 150)
(*b*) Recently hatched cocoons collected in the field	—	—	63
Total parasites (killing one host each)	3	499	218
Percentage of larval parasitism of the actual local population	6·8	35·1	64·5
Limits of confidence for total (k=2)*...	$x^{1} = 2{\cdot}3$ $x^{11} = 18{\cdot}5$	$x^{1} = 32{\cdot}6$ $x^{11} = 37{\cdot}6$	$x^{1} = 58{\cdot}9$ $x^{11} = 69{\cdot}5$
Minimum reduction of population after hibernation†	—	39·5	66·8

**i.e.*, the interval between the "fiducial limits" (Mutungsbereich) that contains the real value with a certainty of 95 per cent. (k=2). See Clopper & Pearson (1934) and von Schelling (1939).

†6·8 per cent. of sample I is added to samples II and III respectively thus taking into account the earlier reduction in population.

generations per annum in the same host species as a result of the prolonged developmental period of *C. histrionana* and the fact that *M. ruficeps* lives during the winter in at least two other species of Microlepidoptera which complete their development earlier. In June and July, *M. ruficeps* concentrates on *C. histrionana* (see p. 15).

Parasitism of Pupae.

As already mentioned, this could not be determined accurately because of the great reduction of the larval population ; only 37 unhatched‡ pupae were found in the field (19th to 27th July). Of these five (13·5 per cent.) were parasitised by the species shown in Table IV. One was attacked by *Amblymerus subfumatus*, in this case behaving apparently as a primary parasite. The final degree of parasitism of *C. histrionana* pupae was probably higher than shown here because not all larvae had pupated at the time of collection and at this stage also it may be assumed that the percentage of parasitism may still increase. The complete elucidation of these points is difficult because the few pupae are well hidden and pupation takes place over a long period.

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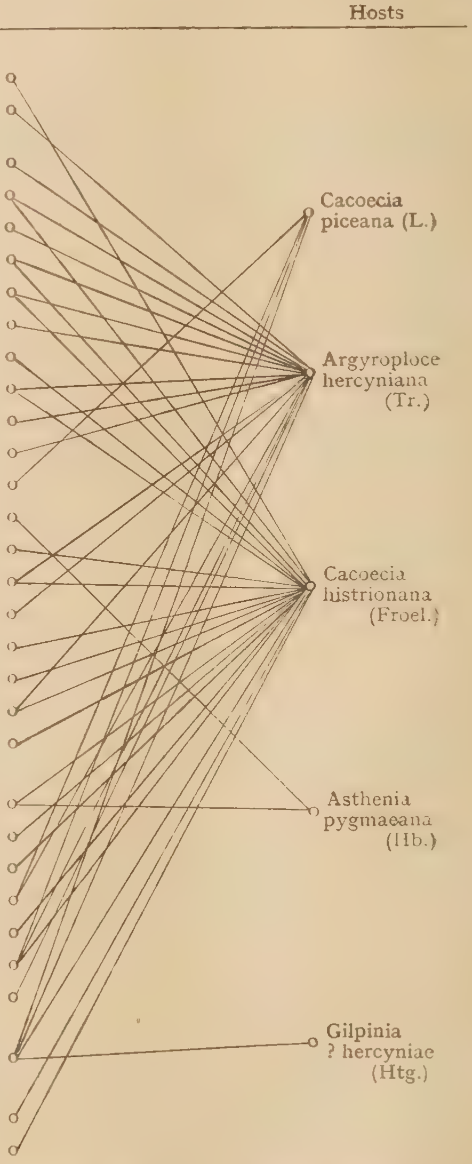
‡Hatched pupae were not collected so that the rate of parasitism has to be calculated from unhatched specimens.

TABLE VI.

Interrelations between Hosts living on Spruce and Parasites, 1949.

(Species reared from *C. histrionana* and a secondary host are marked with an asterisk.)

Status	Parasites
	ICHNEUMONIDAE.
P	*Phaeogenes ? semivulpinus* (Grav.)
P	*Phaeogenes ? fuscicornis* Wesm.
P	*Microcryptus brachypterus* (Grav.) var. *micropterus* (Grav.)
H	**Hemiteles areator* (Panz.)
H	*Hemiteles* spp. (two)
H	**Pezomachus* sp.
P	**Pimpla turionellae* (L.)
P & H ?	*Itoplectis maculator* (F.)
P	*Apechthis resinator* (Thunb.)
P	**Ephialtes pictipes* (Grav.)
P & H ?	*Ephialtes ? detrita* (Hlmgr.)[1]
P & H ?	*Ephialtes brevicornis* (Grav.)
P	*Glypta bipunctoria* (Thunb.)
P	*Triclistus* sp.
P	*Lissonota* sp.
P	**Omorgus mutabilis* (Hlmgr.)
P ?	*Nemeritis* sp.
P	*Angitia rufipes* (Grav.)
P ?	*Angitia* sp.
H	**Mesochorus ? orbitalis* Hlmgr.
P	Tryphoninae, ? genus
	BRACONIDAE.
P	**Apanteles dilectus* (Hal.)
P	*Apanteles xanthostigma* (Hal.)
P	*Apanteles ater* (Ratz.)[2]
P	*Microdus clausthalianus* (Ratz.)
P	*Microdus dimidiator* (Nees)
P	**Meteorus ruficeps* (Nees)
P	*Oncophanes lanceolator* (Nees)
	PTEROMALIDAE.
P & H	**Amblymerus subfumatus* (Ratz.)
	EULOPHIDAE.
P	*Elachertus dimidiatus* (Nees)
P ?	*Tetrastichus ? evanescens* (Ratz.)


Hosts
Cacoecia piceana (L.)
Argyroploce hercyniana (Tr.)
Cacoecia histrionana (Froel.)
Asthenia pygmaeana (Hb.)
Gilpinia ? hercyniae (Htg.)

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[1] According to G. Heinrich the specimens reared (♂♂) differ considerably from true *E. detrita*. Lacking females no final determination was possible.

[2] Reared only 1948 by Groschke.

Parasitism of Eggs.

On 17th October 1949, an egg-mass of *C. histrionana* was found that had been totally parasitised. It was concluded from the dark colour of the egg shells and the very small emergence-holes that *Trichogramma* sp. or a related species had emerged. This indicates that the egg-stage population, also, is reduced by parasites, but the importance of this is as yet unknown.

Secondary Hosts.

From the results of the small sample of 1948 there was reason to conclude that some of the parasites of *C. histrionana* attacked several hosts. To understand the factors determining the natural balance, it was desirable to get more complete information on the correlation existing among the insects living on spruce twigs. Table VI shows the close interrelation of certain members of this animal community (choriocenosis) as far as it has been determined.

Of 19 parasites known hitherto from *C. histrionana*, nine also occur in other hosts in the same habitat, four as hyperparasites (see Table VI). The table of host relations shows the close mutual correlation of parasites and hosts in the spruce forests of the area studied. The true situation is no doubt even more complex. The competition that exists in this insect community on spruce must exercise a considerable influence in preventing any one of the host species from staging an outbreak.

Just as important as the number of parasite species is the attachment of the main parasite of *C. histrionana* to three hosts. *M. ruficeps* seems, according to the available data, to be also the main parasite of the larvae of *Cacoecia piceana* (L.) ; it also played a part in the control of caterpillars of *Argyroploce hercyniana* (Tr.) (parasitism about 20 per cent.), though *Microdus clausthalianus* (Ratz.) which emerged from the older larvae (about 80 to 90 per cent. parasitism of the rest) was the principal parasite of this species. With the larvae of *Asthenia pygmaeana* (Hb.), *Apanteles dilectus* was the main parasite, but this polyphagous species sometimes attacks *C. histrionana* also. The same species was bred, for instance, by the writer from *Semasia rufimitrana* (H.-S.) as the dominant larval parasite in 1948. Other cases of host alternation are indicated in Table VI.

The dominant Parasite.

The life-history of *M. ruficeps* (Nees) has not yet been completely worked out. Considering the possible bearing of the species on biological control, such information as is available is given here. The species was first described by Nees von Esenbeck (1834) from both sexes collected in Thuringia, Germany ; according to Schmiedeknecht (1897) it occurs in Germany and Russia. It lives as an endoparasite in the host larva, and is known from *Calymnia trapezina* (L.) (Lep.) Brischke (1882) and Morley & Rait-Smith (1933) and from *Tinea cloacella* Haw. (Lep.) (Stellwaag, 1924).* G. E. Bucher (unpublished report in 1947–48) refers to it as a larval parasite of *Cacoecia murinana* (Hb.), of minor importance in the Vosges, France, and as being third in importance among the larval parasites in the Black Forest in Germany. Furthermore, there is one specimen in the British Museum, from an unknown Microlepidopteron from larch (Nixon, *in litt.*). Brischke (*l.c.*,

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*In the paper by Stellwaag the species is named *Meteorus ruficeps* Marsh. The specimens were identified by Schmiedeknecht, but in his paper (1897) only Nees is used as the author's name. It may be that the specimens have been labelled " *Meteorus ruficeps* (Nees) Marsh." by Schmiedeknecht. This question must be left unsolved since the collection concerned was destroyed during the war. From the ecological point of view a solution of the problem would be desirable because the habitat of *T. cloacella* in deep wine cellars differs considerably from the living range of the parasite known hitherto.

p. 121) states that the cocoon: "... hängt an einem Faden, ist elliptisch mit dünneren, abgerundeten Enden, in der Mitte am breitesten, fest braun." This is the usual cocoon shape of many species of the genus, but it does not apply to the cocoon of *M. ruficeps* reared in the present study. It seems doubtful, therefore, that the same species is concerned in both cases. No further references to the biology of this species have been seen by the writer. Mr. G. E. J. Nixon of the Commonwealth Institute of Entomology states that there is a good deal of confusion concerning the identity of the numerous species in the genus. This question may, therefore, be left on one side for the present.

The translucent cocoon of *M. ruficeps*, 5–6 mm. long and 1·8–2·0 mm. wide, is longish oval in shape, with relatively pointed ends (Pl. II, *d*, *e*) and a rather rough outer layer. It has a greenish tinge on the first day, that turns yellowish later and finally black due to the colour of the larva and later of the pupa within, since the cocoon itself is without colour. For a coloured picture of Pl. II, *e* showing the parasite cocoon at about 4 days old, see Franz (1950). It is spun by the larva inside the web of the host immediately after leaving the host. The emergence hole is always situated laterally in the abdomen of the host larva, usually on the sixth abdominal segment. The first threads of the *M. ruficeps* cocoon appear while the posterior part of the larva is still inside the host (Pl. III). The host larva lives for several days beside its parasite, on an average for six or seven days in summer and because it ceases to feed, it shrinks in the course of time to the size of the cocoon (Pl. III, *f*). The adult parasite emerges by making a neat circular cut of about 0·7 mm. length in the anterior end and pushing off the lid thus formed which usually remains attached by a narrow hinge. When the hyperparasite *Mesochorus* (?) *orbitalis* hatched, an irregular hole opening laterally was made at one end of the cocoon. The length of the period spent by the *M. ruficeps* larva inside and outside the host depends on temperature, the former period also on the development of the host. Four cases were observed accurately, with several others giving minimum values. The value for development inside the host varies considerably. For example, young larvae of *C. histrionana* attacked by the parasite produced no full-grown parasite larvae until they reached a certain size (see below). Also, during the cooler parts of the season the development of the parasite was obviously delayed. On the other hand, the developmental period within older host larvae averaged 19 days in summer. In addition, the cocoon period lasts about six or seven days, at summer temperatures of 17 to 21°C. Thus, the complete development from the egg, deposited in older larvae, to the adult, takes scarcely four weeks during the summer and correspondingly more in the cooler seasons.

The adults readily drink sugar water and can be kept for weeks at low temperatures. The ratio of females to males in 71 reared specimens was 1·15 : 1. Whether the same sex ratio prevailed in the cocoons sent to Belleville is not known. Mating and oviposition may take place very soon after the hatching of the adults. On 25th July, five *M. ruficeps* cocoons were placed with three unparasitised larvae of *C. histrionana* and on 28th July the adult parasites which had emerged were removed. Subsequent observations showed that the parasites, while not more than three days old, had successfully attacked all three larvae. Successful superparasitism is rare; in only two cases did *C. histrionana* larvae yield two cocoons despite the many hundred single cocoons collected in the field during the latter half of June.

Apparently all instars from the second to the last are attacked by parasites. Groschke (1949) succeeded in getting the second instar attacked in the laboratory. The fact that among 20 of these larvae only one produced a parasite while 11 died, suggests that young larvae frequently die from the attack. In the field, young host larvae are regularly attacked in autumn. The first *M. ruficeps* reared from young overwintering caterpillars collected in the field in October 1949 hatched in a laboratory rearing on 1st February 1950. The parasitism of overwintering larvae, however, is low. Even when they were attacked young the larvae were not abandoned by the parasite larvae before they reached about the seventh instar (head capsule 1 mm.). Three-quarter grown host larvae were usually chosen by *M. ruficeps* ; one instance was observed on 28th June in which the head capsule of the host was 1·4 mm. In addition, this preference is confirmed by the dates of the appearance of the cocoons in the rearings.

A great deal of information was collected about the flight period of the parasite, the presence of an open cocoon indicating readily that the adult had emerged. In the main collecting area the first open cocoons from *A. hercyniana* were found on 24th May, from *C. piceana* on 27th May, and from *C. histrionana* on 1st June. An open cocoon from *C. histrionana* had already been found north-west of Regensburg on 23rd May. The flight period lasts throughout the whole summer, reaching its peak in July and extending until October. A freshly hatched cocoon attached to a still living, full-grown *C. histrionana* larva was found in the main collecting area as late as 17th October 1949.

The other hosts such as *A. hercyniana* (Pl. II, *e*) and *C. piceana* were regularly found in the main collecting area. *A. hercyniana* was about three times as frequent as *C. histrionana* but *C. piceana* was even more rare than *C. histrionana*. Both of the alternate hosts are attacked before hibernation and the parasite was bred from the overwintering larvae of both. These alternate hosts pupate at the beginning or the middle of June, and all *M. ruficeps* hatched from them concentrated on *C. histrionana* which was probably at that time the only host for this species in the area studied. Late in the summer they spread to the next generation of their former hosts. Thus,

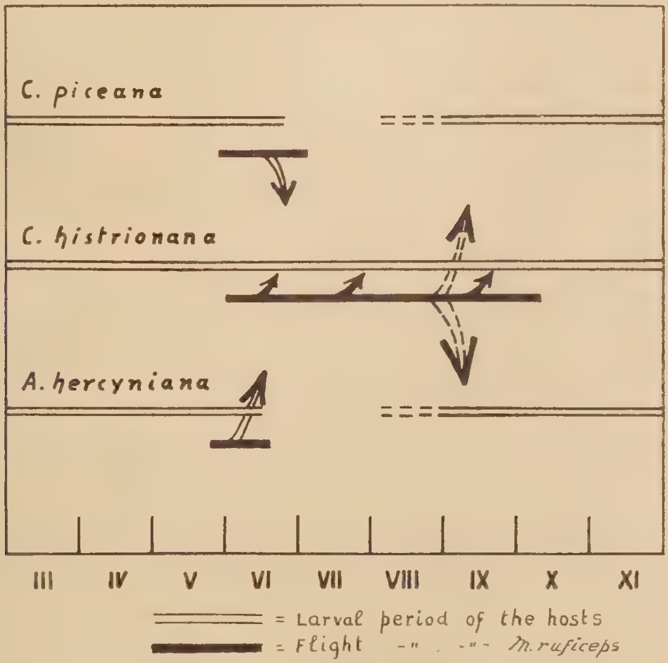

Fig. 2.—Diagram representing alternation of hosts by *Meteorus ruficeps*. The arrows indicate the approximate time and direction of host alternation. The three small arrows on *C. histrionana* intimate the possibility of three generations of the parasite. Broken lines where exact dates unknown. All dates refer to 1949, main collecting area.

the parasite passes the first generation in at least three hosts, the second and certainly part of a third generation also, in one host only. This alternation between hosts is shown diagrammatically in fig. 2 and is one of the reasons why parasitism of *C. histrionana* is so astonishingly high in summer. The sequence of events varies considerably, of course, with climatic conditions and there may be marked deviations in other years. A similar host alternation may, to a certain extent, occur in some of the other parasitic Hymenoptera. *Omorgus mutabilis*, for instance, overwinters in *A. hercyniana*, emerges at the end of May, and part of a second generation develops in *C. histrionana* from which the parasite hatches at the beginning of August.

Predators.

The population density of *C. histrionana* was too low for an extensive inquiry into predator problems. On one occasion, however, a specimen of *Raphidia notata* F. (Neuropt.) determined by V. Weiss, Hamburg, was caught feeding on a caterpillar. This predator was not particularly abundant in the main collecting area.

Diseases.

Neither in the rearings nor in the field was anything like a mass mortality of larvae or pupae noticed. Occasional dead larvae were found which appeared to be infected by a virus disease ; the body was soft and its contents fluid, as is usual with caterpillars that have succumbed to virus diseases. These larvae were collected and shipped to Belleville for further investigation. As far as could be observed the disease played a very small part in causing mortality. The mortality of approximately 20 per cent. during rearing was probably caused by unsuitable living conditions.

Discussion.

In two recent papers, Eidmann (1949a, b) has dealt with *C. histrionana*. The existence of many insect species on useful plants without being economically important is called by him " indifference." To anticipate, this expression seems to be rather misleading as the usefulness or harmfulness of an animal has no absolute value. A fruit feeding insect, for instance, on a tree which is utilised as timber only, is " indifferent " ; if, however, the fruits are desired, the species acquires the status of a pest.

Eidmann probably means by " indifference " the fact that but few of the many insect species, living on a cultivated plant, ever occur in very large numbers, most of them remaining relatively inconspicuous and at a low population density ; as an example he mentions *C. histrionana*. He gives a distribution map showing all localities where moths were known to have been caught, together with the occurrence of its main host plant, the spruce. This indicates that no specimens are known from the spruce region east of the Weichsel river (now Poland), and that *C. histrionana* occurs in southern France some 100 km. beyond the western limits of the natural spruce. In view of this he concluded that the potential range of *C. histrionana* ends near the Weichsel River, and that its climatic optimum lies outside the actual living range, in warmer zones. In this way, he explained the relative scarcity of the Tortricid as determined by climatic factors. The possibility that it is due to natural enemies, he regarded as improbable " because, according to all experience gathered hitherto, their effect in reducing populations cannot act until a relatively high density of population is reached " (1949a, p. 363).

The following facts do not support this theory. Firstly, the known north-easterly limit of the range of *C. histrionana* is very uncertain owing to the very inadequate knowledge of Polish and Russian Microlepidoptera and this opinion has been kindly endorsed by Dr. M. Hering of the Berlin Museum. One is therefore not justified in correlating it with climate. Secondly, in checking the natural reproductive potential, climatic and biotic factors always act together. Therefore, it is very difficult to set up a climatic theory in the absence of knowledge regarding the natural enemies. A distribution map, as far as it is correct, only indicates the net result of the various regulating factors, including historical processes. No conclusions attributing causes to single factors should be drawn from such a map.

Since the highest relative abundance of the species occurs at elevations ranging from 650 to 800 m., it does not seem very likely that it finds optimum conditions only in warm zones. Its thermal adaptation does not seem to be very restricted; otherwise it could not exist, as it does, over an area extending from southern France to the mountainous regions of the Carpathians and other higher areas. Eidmann was not aware that many parasites play a part in checking the population of *C. histrionana*, and that this is done very effectively has been shown in the present work.

The problem of "indifference" is basically nothing else but the problem of natural balance, or better, of natural control (Solomon, 1949) in cultivated plant communities, and it is not proposed to make a more detailed study of it here. The evidence provided by the present work makes it possible, however, to put forward some conclusions on the regulation of the density of *C. histrionana*.

In spite of the relatively moderate density of the population in some areas (see p. 7) the number of eggs laid per female is approximately 100 (Eidmann, 1949b) and theoretically an outbreak could occur on occasions. Of the controlling factors investigated in 1948, 1949, and 1950, parasites were particularly effective. Their effectiveness was increased by the concentration of parasites due to the temporary disappearance of other hosts and by the widely varying length of development of *C. histrionana* without diapause, so that host larvae were available all the year round. The conclusion is that high parasitism, promoted by various favourable biological conditions, seems to be of particular significance in checking the growth of the population, despite its comparatively low level. The whole complex requires much further work in order to check the results by making observations in other areas, in other years, and in applying additional methods.

A comparison of *C. murinana* and *C. fumiferana* with *C. histrionana* will probably indicate the ecological importance of diapause in the two first mentioned. In these two species, development is synchronised almost completely every year. After a long pause in a sheltered hiding place renewed feeding in a comparatively exposed locality starts in the spring, and is of much shorter duration than that of *C. histrionana*. For these reasons it is not surprising that no parasite is known which completes more than one generation in either of the spruce budworms, such as has been shown for *M. ruficeps* in *C. histrionana*. The highest percentage of parasitism, found by Wilkes and others (1949) for one parasite obtained from larvae of *C. fumiferana* in British Columbia, is 5·7 per cent. (relative abundance of *Glypta fumiferanae* (Vier.), 1943–1947). In the case of *C. murinana*, the writer (Franz, 1940–41) found that approximately 15 per cent. is the maximum value for one larval parasite (*Glypta murinanae* Bauer, 1939 in the Black Forest). These figures are markedly lower than those for *M. ruficeps* on *C. histrionana*.

How *M. ruficeps* will stand the test of importation into Canada remains to be seen. It will certainly be necessary to take into account the great differences between the hosts, and the need of the parasite to complete several generations a year, before it is possible to estimate its probable efficacy against the Canadian spruce budworm.

Summary.

Cacoecia histrionana Froel. a European relative of the North American spruce budworm, *Choristoneura fumiferana* Clem., was found in several localities on the north-eastern frontier of Bavaria in 1949, but was not abundant anywhere.

Details are given of its biology based upon observations made during large-scale collecting in the summer of 1949, which yielded approximately 2,100 larvae of *C. histrionana*.

An important characteristic of the species is the great variation in the stages of larval development present at any given time, which is apparently caused chiefly by the absence of diapause as a synchronising factor.

Approximately 4°C. was found to be the lower temperature limit for movement and feeding of larvae ready for overwintering.

Three samples of larvae taken in favourable localities showed that 0·15 to 0·70 larvae were present per metre length of spruce forest edge from ground level to a height of 2 metres. An estimate of the minimum population is made for a limited and well searched area.

From 1803 *C. histrionana* larvae collected in the field, 15 species of primary parasites and four of hyperparasites were bred. Combining the result of three samples taken at different times the minimum reduction of the population after hibernation is calculated to be 66·8 per cent., the parasitism of pupae at least 13·5 per cent. Egg parasitism occurred.

Nine of the 20 parasites, known hitherto from *C. histrionana*, have been bred from other hosts of the same animal community.

The most important larval parasite was *Meteorus ruficeps* Nees which completes 2–3 generations in one generation of *C. histrionana*. A proportion of the population also overwinters in other Microlepidoptera, concentrating on *C. histrionana* in summer. Details of its life-history are given.

Occasionally some larvae were found that had probably died from disease but disease, as a mortality factor, was of little consequence in the observation area in 1949.

Mortality caused by parasites proved to be very important in affecting changes in the population density. This result does not agree with Eidmann's theory that the scarcity of *C. histrionana* is due to climatic control.

Acknowledgements.

Thanks are expressed to Mr. H. Wichmann for his valuable assistance in the field work. The writer is indebted to Dr. C. Ferrière, of Geneva, for identifying all parasites collected. Special thanks are due to Dr. K. Boening, in charge of the Department of Plant Protection of the Bavarian Landesanstalt für Pflanzenschutz, Munich, for permission to use his laboratory for some experiments. Other experts, particularly on parasitic insects, including Dr. H. Sachtleben, director of the German Entomological Institute at Berlin, Dr. J. Fahringer, Vienna, G. E. J. Nixon, Commonwealth Institute of Entomology, London, and G. Heinrich, Dryden, Maine, U.S.A., have helped greatly by offering useful suggestions and by providing details of relevant literature.

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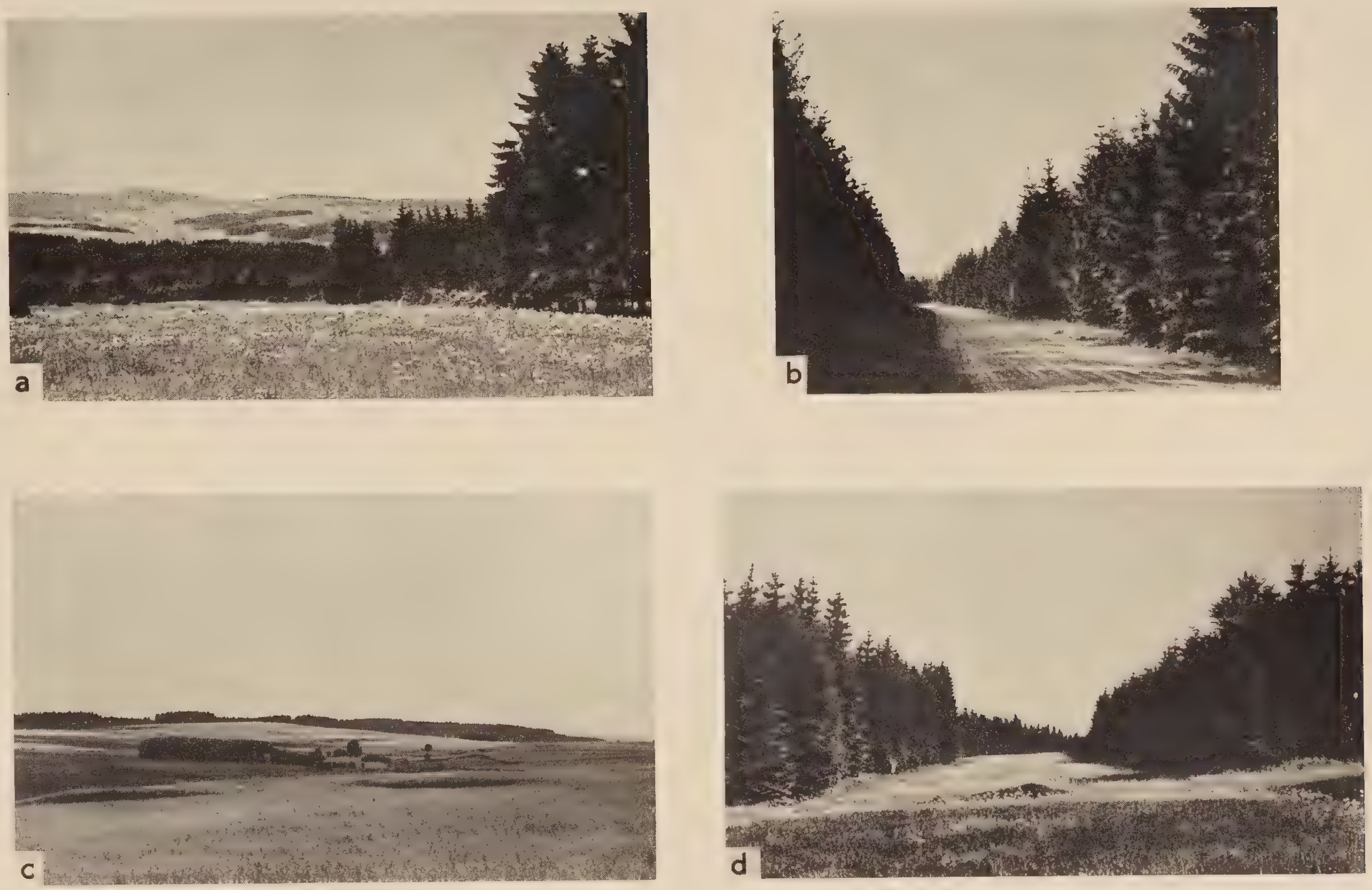
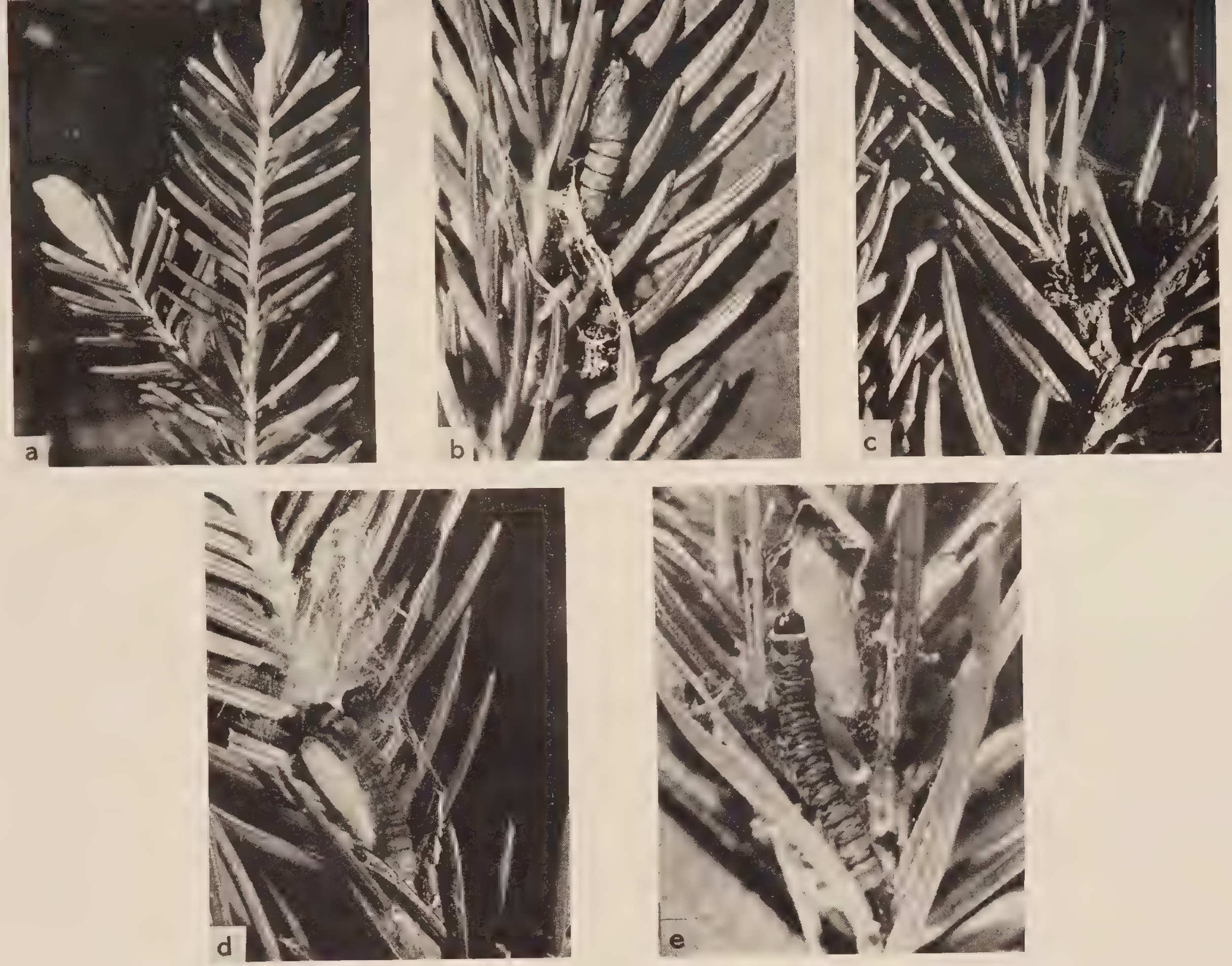
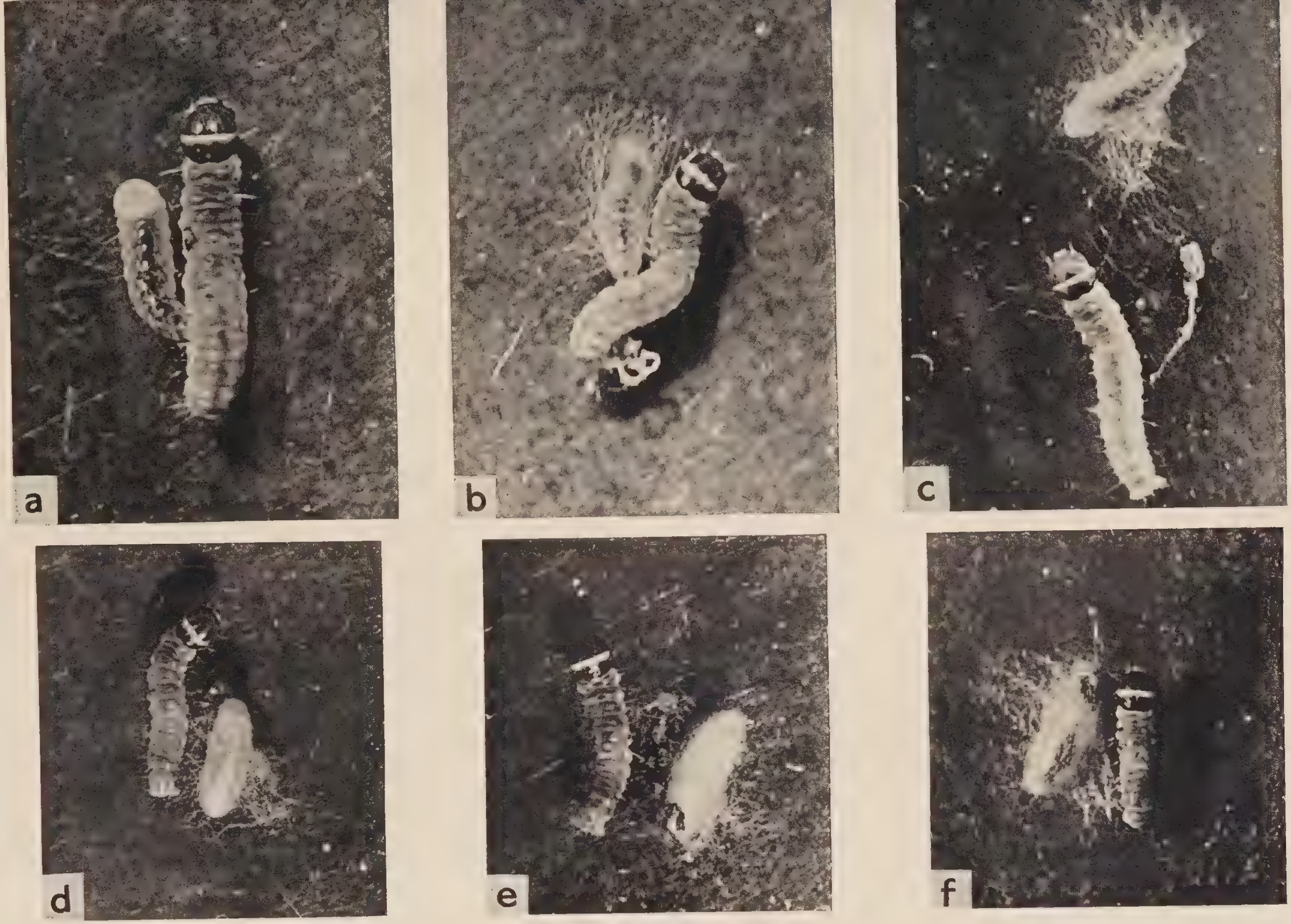


(*a*). View from Poppenreuther Berg looking to the south west. Typical landscape of the main collecting area; (*b*), road with pole-stands north of Baernau; typical *C. histrionana* infestation; (*c*), small isolated plantation inhabited by *C. histrionana* and *M. ruficeps* 1140 m. distant from the nearest forest; (*d*), counting place No. 3, Poppenreuther Berg. Note the man's size.



(*a*), Feeding place (on the upper bud) and hiding place (centre) of an almost full grown larva of *C. histrionana* in the spring; (*b*), pupa of *C. histrionana* under the remains of the larval skin; web opened (x 2·5); (*c*), hibernating web of *C. histrionana* on spruce. The pale needles have been freshly mined (x 2·5); (*d*), opened web of *C. histrionana* showing the larva still alive and the cocoon of *M. ruficeps*, about two days after emergence from the host (x 2·5); (*e*), opened web of *Argyroplace hercyniana* showing the living larva and the cocoon of *M. ruficeps*, about four days after emergence from the host (x 5·5).



Larva of *M. ruficeps* emerging from *C. histrionana.* (*a*), and (*b*), parasite larva although not yet fully emerged already spinning the outer layer of the cocoon; (*c*), four hours later than *a*, cocoon still transparent greenish, last frass-pellet and a piece of the caterpillar's web; (*d*), nineteen hours later; (*e*), four days later, parasite after pupation; (*f*), six days later, parasite shortly before hatching, host larva dead (x 3-4).

PIPERONYL BUTOXIDE AS A CONSTITUENT OF HEAVY-OIL SPRAYS FOR THE CONTROL OF STORED PRODUCT INSECTS.

II.—THE EFFECT OF PIPERONYL BUTOXIDE ON THE TOXICITIES OF ALLETHRIN, DDT, AND BHC, AND ON THE JOINT TOXICITY OF BHC AND PYRETHRINS, TO *TRIBOLIUM CASTANEUM*.

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The preceding paper (Hewlett, 1951) described, among other things, some investigations into the synergism between piperonyl butoxide and pyrethrins, in solution in Shell oil P31. This paper is concerned with the effects of piperonyl butoxide on the toxicities to the flour beetle, *Tribolium castaneum* (Hbst.) of allethrin, DDT, and BHC, and on the joint toxicity of BHC and pyrethrins. P31 was again the solvent. Technical piperonyl butoxide is referred to as PB.

Materials and Methods.

Allethrin is the coined name (Rohwer, 1950) for the completely synthetic allyl homologue of cinerin I, now being prepared commercially in the U.S.A. (Stoddard & Dove, 1949). The solutions of allethrin were obtained by diluting a sample, probably containing about 90 per cent. by weight of the pure material ; the concentrations refer to the impure material. The DDT used was the pure p,p′-compound and the BHC the pure gamma isomer. The concentrations of PB are expressed as %v/v, whereas those of the other materials are expressed as %w/v. The small systematic error introduced by the different specific gravities of PB and P31 (see Hewlett, 1951, p. 295) was again not allowed for, unless otherwise stated. The concentrations of DDT and BHC were made higher in the direct spray than in the film tests, so as to obtain suitable ranges of mortality.

The test insects were adult *T. castaneum* bred and prepared for tests as previously described (Hewlett, 1951). The beetles were either exposed on films on filter paper at 25°C. by the technique of Parkin and Green (1943), or were directly sprayed by that of Hewlett (1947) at 20–21°C., and afterwards kept at 25°C. The relative humidity was 70 per cent. The response in the groups of beetles was determined six and nine days after the start of their exposure to insecticide, using the same criteria as previously (Hewlett, 1951).

Results.

In considering the data now presented it should be remembered that Hewlett (1951) found that PB in P31, over the range of doses used in the experiments to be described, was virtually non-toxic to *T. castaneum* as direct sprays, and as films after exposure for six days ; but appreciably toxic as films after exposure for nine days.

An experiment with allethrin.

A small-scale experiment was carried out to compare the toxicity of 3·5 per cent. allethrin+5 per cent. PB with that of 3·5 per cent. allethrin alone. Both methods of application were used, and Table I shows the results. Obviously the PB synergized the allethrin, in both films and direct sprays.

Experiments with DDT and BHC.

In all the experiments with DDT and BHC the knock-down was but little higher than the mortality, and so only the latter is recorded.

The results of a preliminary experiment, in which beetles were exposed to direct sprays of 2·0 per cent. DDT or 1·5 per cent. BHC, with or without 5 per cent. PB, were confirmed by a similar experiment of which the results appear in Table II. These show that PB increased the toxicity of the BHC, but left that of the DDT unchanged.

TABLE I.

The toxicity to *Tribolium castaneum* of allethrin, alone or with piperonyl butoxide.

Technique	Insecticide	Number of beetles	Deposit mg. /10 sq. cm.	Knockdown %		Mortality %	
				6 days	9 days	6 days	9 days
Film ...	3·5% allethrin	50	16·44	80	80	40	58
		50	22·60	84	94	66	74
	3·5% allethrin + 5% PB	50	17·38	100	100	100	100
		50	22·88	100	100	100	100
Direct spray	3·5% allethrin	50	4·00	10	10	8	10
		50	8·00	38	40	36	40
	3·5% allethrin + 5% PB	50	4·00	92	92	82	92
		49	8·00	100	100	87·8	100
—	Control	200	—	0·5	1·0	0·5	1·0

TABLE II.

The toxicity to *Tribolium castaneum* of direct sprays of DDT and BHC, alone or with piperonyl butoxide, as shown by mortalities in batches of 48–51 beetles.

Insecticide	Deposit mg. /10 sq. cm.	Mortality %			
		6 days		9 days	
		Insecticide alone	With 5% PB	Insecticide alone	With 5% PB
2·0% DDT ...	4·00	53	46	59	48
	6·07	61	58	69	58
	9·20	78	80	78	84
	14·00	82	92	88	94
1·5% BHC ...	1·58	12	37	16	41
	2·51	60	68	60	72
	3·98	72	100	74	100
	6·31	76	98	82	100
Control* ...	–	0		2	

*200 beetles.

Another experiment was performed to see whether PB would synergise 0·6 per cent. DDT as a film. The PB concentration was raised to 10 per cent., to reduce the chances of missing any synergistic effect. The results shown in Table III make it clear that PB antagonised DDT as a film, an unexpected result which a further test confirmed.

TABLE III.

The toxicity to *Tribolium castaneum* of films formed by DDT, alone or with piperonyl butoxide.

Insecticide	Number of beetles	Deposit mg./10 sq. cm.	Mortality %	
			6 days	9 days
0·6% DDT	50	13·53	42	50
	50	17·35	56	78
	50	19·90	84	96
	50	22·57	86	98
0·6% DDT+10% PB	49	13·80	8·2	32·7
	50	17·20	28	44
	50	19·84	52	56
	50	22·52	72	78
Control	200	—	0	0·5

Further experiments were carried out to gain additional information on the synergism between PB and BHC. Their design was influenced by the fact that they were conceived as steps towards discovering whether PB would synergise pyrethrins and BHC simultaneously (see p. 25). In a film test the toxicities of 0·05, 0·1, and 0·2 per cent. BHC were compared with those of the same concentrations of BHC with 2·5 per cent. PB. Table IV gives the results.

Inspection of Table IV indicates that as films PB synergised BHC slightly. The data were examined graphically by plotting probit mortality against log.-deposit,

TABLE IV.

The toxicity to *Tribolium castaneum* of films formed by different concentrations of BHC, alone or with 2·5 per cent. piperonyl butoxide.

BHC %	PB %	Number of beetles	Deposit mg./10 sq. cm.	Mortality %	
				6 days	9 days
0·05	—	50	10·03	8	10
		50	13·43	14	18
		49	19·92	22·4	30·6
0·05	2·5	50	9·76	8	16
		50	14·05	22	24
		50	19·53	42	48
0·10	—	49	10·03	46·9	51·0
		50	14·52	52	66
		50	20·13	70	74
0·10	2·5	50	10·54	46	50
		50	13·25	60	72
		50	19·77	74	84
0·20	—	50	9·61	78	86
		50	13·84	86	90
		50	19·90	92	96
0·20	2·5	50	9·95	90	92
		50	13·77	96	98
		50	19·84	98	98
Control		200	—	0	0

and it was then obvious that the increase in mortality due to the PB was significant. The effect of the PB tended to be a little greater on the 0·2 per cent. BHC than on the other BHC concentrations ; but the data for each observation period could be represented by two parallel probit planes in log.-concentration of BHC and log.-deposit, one plane for BHC alone and the other for BHC+PB. The probit difference between each pair of planes was about 0·35, and the addition of 2·5 per cent. PB effectively multiplied the concentration of BHC by about 1·25. Despite the appreciable mortality produced by PB alone after 9 days' exposure of the beetles (Hewlett, 1951), the PB-BHC mixtures were not detectably more toxic relative to the BHC alone at 9 days than at 6 days. This effect was thus similar to that with films of PB and pyrethrins, and is explicable on the same basis (see Hewlett, 1951, p. 295).

A direct spray experiment, the data from which are not given, yielded parallel probit-log.-deposit regression lines for 1·25 per cent. BHC alone and for 0·25, 0·50, and 1·00 per cent. BHC each with 2·5 per cent. PB. Graphical analysis indicated that 0·7 per cent. BHC+2·5 per cent. PB was about equivalent to 1·25 per cent. BHC alone, and hence the PB effectively multiplied the BHC concentration by roughly 1·8. In a further direct spray experiment the deposit was kept constant at 5·00 mg. /10 sq. cm., and the toxicities of 0·50 per cent. and 1·00 per cent. BHC alone were compared with those of 0·25 per cent., 0·50 per cent., and 1·00 per cent. BHC each combined with 2·5 per cent., 5·0 per cent., and 10·0 per cent. PB. It was found, however, that variation of the concentration of PB over this range did not influence the toxicity of the mixtures, and hence in Table V the mortalities for the three PB concentrations have been averaged.

The results of Table V for each observation period could be represented by two parallel probit-log.-concentration regression lines, one for BHC alone and the other for BHC+PB. The parallel lines for the 6-day observations were computed, by the methods described by Finney (1947), as

$$\text{BHC} \quad \ldots \quad Y=5{\cdot}61+4{\cdot}64x$$

$$\text{BHC+PB} \quad Y=6{\cdot}64+4{\cdot}64x$$

where Y is probit mortality and x is log.-concentration of BHC. Fitting these parallel lines gave $\chi^2=1{\cdot}40$ on 2 degrees of freedom, whence P=0·49. The potency of the BHC+PB relative to the BHC alone was thus estimated as 1·66, but its 5 per cent. fiducial limits were 1·51 and 1·83, so it agreed substantially with the rough figure of 1·8 from the preceding experiment. In particular, the relative potency of 1·66 indicated that in direct sprays 0·5 per cent. BHC alone was equivalent to 0·3 per cent. BHC+2·5 per cent. PB, an equivalence confirmed by direct comparison

TABLE V.

The toxicity to *Tribolium castaneum* of direct sprays of BHC alone or with piperonyl butoxide at 2·5, 5, and 10 per cent.* : deposit 5·00 mg. /10 sq. cm.

Insecticide	Number of beetles	Mortality % after	
		6 days	9 days
0·50% BHC	150	20·0	25·3
1·00% BHC	149	75·2	77·2
0·25% BHC+PB ...	298	12·4	18·1
0·50% BHC+PB ...	299	60·9	63·5
1·00% BHC+PB ...	300	94·0	94·7
Control...	200	0·0	0·5

*Since varying the concentration of PB over this range did not influence the mortality, the results for the three PB concentrations have been pooled.

of the toxicities of the two solutions and used in succeeding experimental work (see below).

The relative potency of 1·66 corresponded to a probit difference of 1·02, and hence 2·5 per cent. PB synergised 0·5–1·0 per cent. BHC in a direct spray more strongly than it did 0·05–0·20 per cent. BHC in a film, whether judged by relative potencies or probit differences.

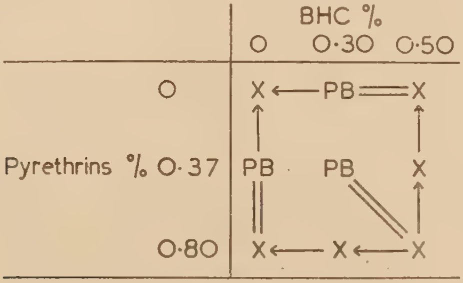
The effect of piperonyl butoxide on the joint toxicity of BHC and pyrethrins.

Since Hewlett & Plackett (1950) had shown that mixtures of BHC and pyrethrins are very much more toxic to *T. castaneum* than either insecticide alone, and since PB was found to synergise each insecticide, it was natural to enquire whether PB would synergise the two insecticides when mixed. The experimental requirements for testing this were stringent, and the experimental design was complicated, compared with what was necessary for showing that PB synergised each insecticide separately. The design of the experiments can be most easily explained by reference to the particular insecticides and concentrations used, but the general case follows easily enough. The direct spray method was employed because PB synergised BHC more intensely by this method of application. Moreover, PB alone was non-toxic in direct sprays, and the experimental design used in testing for the simultaneous synergism demanded that PB alone should be non-toxic.

In direct sprays, as mentioned above, 0·30 per cent. BHC+2·5 per cent. PB was found equivalent to 0·50 per cent. BHC. Other (unpublished) data indicated that 2·5 per cent. PB+0·37 per cent. pyrethrins was equivalent to 0·80 per cent. pyrethrins. If, therefore, the PB in a formulation containing 0·30 per cent. BHC+2·5 per cent. PB+0·37 per cent. pyrethrins synergised each of the two insecticides as though the other were absent, this triple formulation would be expected to be of the same toxicity as 0·50 per cent. BHC+0·80 per cent. pyrethrins. This illustrates what is meant here by the term "simultaneous synergism". However, in order to prove such synergism it is necessary to show that the test method is sensitive enough to reveal 0·50 per cent. BHC+0·80 per cent. pyrethrins as significantly more toxic than either 0·50 per cent. BHC+0·37 per cent. pyrethrins or 0·30 per cent. BHC+0·80 per cent. pyrethrins, since otherwise the PB in the triple formulation might be synergising one of the insecticides only. As a further check on the technique it is advisable to show that 0·30 per cent. BHC+0·80 per cent. pyrethrins and 0·50 per cent. BHC+0·37 per cent. pyrethrins are respectively more toxic than 0·80 per cent. pyrethrins alone and 0·50 per cent. BHC alone. Lastly, as a formal condition, 0·30 per cent. BHC+2·5 per cent. PB and 0·37 per cent. pyrethrins+2·5 per cent. PB must both give higher mortalities than those in the controls, since otherwise their

TABLE VI.

The experimental design for testing whether piperonyl butoxide synergised BHC and pyrethrins simultaneously. For explanation see text.



respective equivalences with 0·50 per cent. BHC and 0·80 per cent. pyrethrins are not demonstrated.

The experimental design is illustrated in Table VI. The entries in the body of the table represent the different formulations used. The entry " X " signifies a formulation containing no PB, and " PB " one containing PB at 2·5 per cent. Strictly speaking the (0,0) entry should refer to P31 alone, but in fact refers to untreated controls, which is justifiable because the P31 was non-toxic. The double bars and arrows represent the relative toxicities of a set of formulations required to demonstrate simultaneous synergism. A double bar between two formulations means that they are equally toxic, while an arrow points to the less toxic. Further arrows could be filled in, pointing outward from the central entry, but these would be the automatic consequences of the relativities shown, and so would be in a sense redundant. In the general case the same relativities as those shown in Table VI would need to be satisfied.

Two experiments of the design described were carried out, and Table VII shows their results. The deposit was kept constant at 5·00 mg./10 sq. cm., except for the solutions containing PB, for which it was raised to 5·03 mg./10 sq. cm. in order to allow for the specific gravity of the PB. Three batches of about 50 beetles were sprayed with each solution, and for nearly every treatment the agreement within the set of three mortalities was satisfactory.

Although 0·37 per cent. pyrethrins+2·5 per cent. PB had previously been found equivalent to 0·80 per cent. pyrethrins alone, in the first experiment the former gave significantly higher mortalities than the latter (by χ^2 tests P=0·023 approx.). The former had been used at 5·00 mg./10 sq. cm., but the increase of 0·03 mg./10 sq. cm. was much too small to account for this difference in mortality. Accordingly an experiment was carried out on a larger scale than previously to re-determine the pyrethrin equivalent of 0·37 per cent. pyrethrins+2·5 per cent. PB, incidentally adjusting the deposit for the specific gravity of PB: this indicated that this pyrethrin-PB mixture was in fact equivalent to 0·80 per cent. pyrethrins. The experiment for testing for the simultaneous synergism was therefore repeated with the same mixtures as before, and the results are recorded under " Second experiment " in Table VII. Once again, however, the mortality at 6 days due to 0·37 per cent. pyrethrins+2·5 per cent. PB was significantly higher (P=0·0032) than that due to 0·80 per cent. pyrethrins, though at 9 days the difference was not significant (P=0·20).

TABLE VII.

The percentage mortalities in groups of 145–151 *Tribolium castaneum*, produced by direct sprays of different formulations of BHC and pyrethrins, some containing in addition piperonyl butoxide at 2·5 per cent. (percentages in italics).

Observation	Pyrethrins per cent.	First experiment			Second experiment		
		BHC per cent.			BHC per cent.		
		0	0·30	0·50	0	0·30	0·50
6 days	0	0·5†	*17·3*	24·0	0·5†	*28·0*	30·0
	0·37	*18·7*	*79·4*	41·3	*16·8*	*80·7*	56·0
	0·80	7·4	54·3	74·5	5·4	62·8*	77·7
9 days	0	1·5†	*24·0*	28·6	2·5†	*33·3*	36·0
	0·37	*31·4*	*83·9*	47·3	*27·5*	*84·0*	61·3
	0·80	18·0	63·0	77·8	18·8	70·3*	83·1

*Probably high owing to heterogeneity.
†200 beetles.

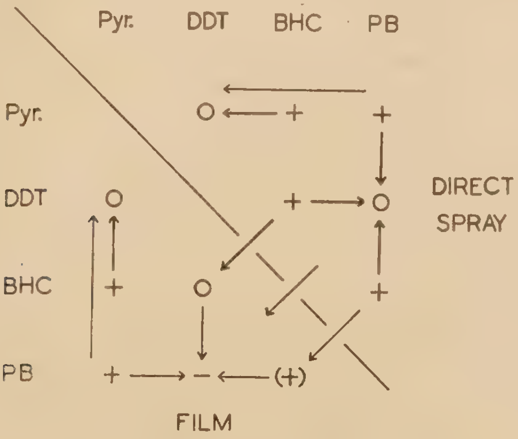
With the exception of that between the pyrethrin-PB mixture and the pyrethrins alone, in Table VII all the relativities of Table VI were satisfied within the limits of sampling error. Where, however, the mixture gave significantly higher mortalities than the pyrethrins alone, the triple mixture tended to give higher mortalities than the 0·50 per cent. BHC+0·80 per cent. pyrethrins ; which, as inspection of Table VI shows, would be expected if simultaneous synergism had occurred. Moreover, at 9 days in the second experiment the mortality for the pyrethrin-PB mixture was not significantly different from that for the pyrethrins alone ; and, correspondingly, the mortality for the triple mixture was then nearly equal to that for the 0·50 per cent. BHC+0·80 per cent. pyrethrins. Therefore although the results were not as clear-cut as had been hoped, Table VII strongly indicates that PB does synergise BHC and pyrethrins simultaneously, *i.e.*, in a mixture of the three, PB synergises each insecticide as though the other were absent. It was clear at least that the presence of either insecticide did not reduce greatly the synergistic effect of PB on the other.

Discussion.

That PB synergised the action of allethrin on *T. castaneum* was not unexpected : allethrin is very similar chemically to the pyrethrins (*sensu lato*). PB has been shown to synergise allethrin in space sprays tested against *Musca domestica* L. (Bishopp, 1950), and in dusts against *Periplaneta americana* (L.) (Piquett, 1949). The data of Jones, Schroeder & Incho (1950), taken in conjunction with those of Stoddard & Dove (1949), indicate that PB also synergised allethrin in direct sprays applied to *Blattella germanica* (L). However, some preliminary tests described by Bishopp suggested that PB was generally a less effective synergist for allethrin

TABLE VIII.

The joint toxicities to *Tribolium castaneum* of mixtures of pyrethrins, DDT, BHC, and piperonyl butoxide, taken in pairs, applied as films or direct sprays in Shell oil P31 : Results taken from Hewlett & Plackett (1950) and the present papers.

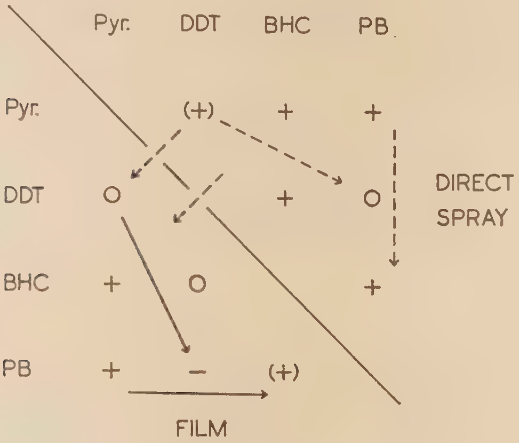


Joint toxicity	*Signs**
Expected on the basis of independent action ...	O
Considerably above this expectation	+
Slightly above this expectation	(+)
Below this expectation	−

*For explanation of the arrows, see text.

TABLE IX.

The joint toxicities given in Table VIII, with further comparisons.



	Pyr.	DDT	BHC	PB
Pyr.		(+)	+	+
DDT	O		+	O
BHC	+	O		+
PB	+	−	(+)	

DIRECT SPRAY
FILM

Note.—The entry of pyrethrins + DDT (direct spray) as " (+) " instead as " O " in Table VIII is explained in the text.

than for pyrethrins, and under some conditions PB synergised pyrethrins but did not synergise allethrin at all. The tests reported here did not permit a comparison between the synergistic effects of PB on allethrin and pyrethrins.

Quantitatively the synergism reported here between PB and BHC resembled that between PB and pyrethrins. Mixtures of PB with either insecticide gave probit-log.-deposit regression lines parallel to the line for the insecticide alone (for the effect with pyrethrum, see Hewlett, 1951). Moreover, films formed by pyrethrins-PB mixtures appeared to be no more toxic relative to pyrethrins alone at the 9-day than at the 6-day observation, despite the toxicity of PB alone at 9 days (Hewlett, 1951), and the effect with BHC was similar. This suggests that the physiological mechanism by which PB synergises the pyrethrins may be comparable to that by which it synergises BHC. Hewlett and Plackett (1950) found that a mixture of BHC and pyrethrins was generally more toxic than if the two insecticides acted independently, and Hewlett (unpublished) has found that such a mixture was more toxic than if they acted similarly in the sense of Bliss (1939). The separate and simultaneous synergism of BHC and pyrethrins by PB may be in some way bound up with the probable synergism between the two insecticides ; but how is at present obscure, and is being investigated. In clearing up the point it would doubtless be helpful to know how PB synergises the pyrethrins. Chamberlain (1950) obtained some evidence that the pyrethrins are detoxified by lipase, and that PB suppresses this detoxification, but his results were inconclusive.

Tests on insecticides all too often yield specific, inconsistent, and incoherent results. For example, the relative toxicity of two insecticides very often differs, indeed may be reversed, according to the species of test insect or the method of application of the insecticide. The results of the present investigation appear to be typical. Thus, in tests with *T. castaneum*, PB synergised pyrethrins strongly in both films and direct sprays ; it synergised BHC, but apparently much more strongly in direct sprays than in films ; and it did not influence the action of DDT in direct sprays, but in films antagonised it. Hewlett and Plackett (1950), investigating the joint actions of pyrethrins, DDT, and BHC, taken in pairs, obtained results of a similar inconsistency. Thus, they showed that in their tests pyrethrins and DDT could have acted independently, but if so the correlation in resistance was positive for the films but negative for the direct sprays ; DDT and BHC could have acted independently as films but not as direct sprays ; and BHC and pyrethrins could not have acted independently for either method of application. Nevertheless an over-all examination of the two sets of results, for PB with the three insecticides and the latter with each other, proves most illuminating.

The conclusions from the two lines of work are very suitable for examination together. The test insect, the two methods of application, and the oil solvent (P31) for the insecticides, were the same throughout. Furthermore, the joint toxicity of the pairs of constituents could be judged according to a uniform standard : the toxicity of every mixture could be described as greater than, equal to, or less than that predicted on the assumption of independent joint action (Plackett & Hewlett, 1948). This standard applies to the tests with PB, because (except after long exposure of the beetles on films) the PB alone was virtually non-toxic, and hence the toxicity, predicted under independent action, of a mixture of PB with any of the insecticides, was that of the insecticide alone.

The results of the two investigations have been entered in Table VIII, those for films in the bottom left-hand portion of the table, and those for direct sprays in the top right-hand. The joint toxicities of the different mixtures, relative to that expected on the assumption of independent action, are entered as signs, " + ", " O ", etc., to which a key is given beneath the table (the meaning of the arrows is explained below). The results for the combinations with pyrethrins are the same for direct sprays and films, but otherwise the film and direct spray conclusions appear inconsistent if the signs, *i.e.*, the joint toxicities, are considered by themselves.

When, however, the joint toxicities are compared with one another, the picture is altered. Two types of comparison can usefully be made, namely (1) between the joint toxicities of pairs of materials applied in the same way and possessing a common member, and (2) between those of the same pair applied by the two methods. Comparisons between the signs are shown in Table VIII by arrows, each pointing to the sign indicating the lower joint toxicity : the arrows for the second type of comparison run, of course, through the diagonal of the table separating the film results from the direct spray.

(1) Of the comparisons of the first type fewer could be made within the direct spray results than within the more differentiated film results. Hence arrows were drawn in the direct spray portion of the table, and the corresponding arrows entered in the film portion where possible. It was then evident that all the comparisons within the film results were in the same direction as those in the direct spray, except that in the former there was no contrast between DDT+BHC and DDT+pyrethrins. Thus, but for this one exception, omitted from Table VIII, the arrows for the films formed a mirror image of those for the direct sprays, the diagonal between the two parts of the table representing the mirror.

(2) Three comparisons of the second type (between methods of application) could be indicated by three diagnonal arrows all pointing in the same direction.

In view of the regularity that had become apparent, the findings of the two investigations were re-examined. Further comparisons were found possible and these are shown in Table IX by pecked arrows.

(*a*) Although Hewlett and Plackett (1950) found that pyrethrins and DDT could have acted independently as both films and direct sprays, if the insecticides really did so the coefficient of correlation in resistance would be positive for films and negative for direct sprays. This is not a plausible interpretation, as Hewlett and Plackett point out, and it seems probable that if these two insecticides acted independently as films there was a slight positive interaction between them as direct sprays. Thus the result for pyrethrins+DDT applied as a direct spray can more reasonably be entered as "(+)", and this has been done in Table IX. Two pecked arrows can then be drawn as shown, with a corresponding continuous arrow between the entry for pyrethrins+DDT and that for DDT+PB as films.

(*b*) On examining the mortalities for BHC+pyrethrins recorded by Hewlett and Plackett, it appeared that the observed mixture mortalities for the direct sprays were definitely higher, relative to the highest predictable by independent action, than those for the films. This is reflected in the probabilities that Hewlett and Plackett record in their Table VII for this pair of insecticides, and the different statistical procedures they had to adopt in analysing the 9-day results for the two methods of application. This permitted a further pecked arrow to be drawn, through the diagonal of Table IX.

(*c*) In direct sprays 2·5 per cent. PB effectively multiplied the concentration of 0·65 per cent. pyrethrins by about 2·0 (Hewlett, 1951), and that of 0·37 per cent. pyrethrins by about 2·2 ; these relative potencies correspond to a probit difference of roughly 2·1. PB at the same concentration effectively multiplied concentrations of 0·25–1·00% BHC by 1·7, corresponding to a probit difference of 1·0. It seems, therefore, that PB at this concentration synergises pyrethrins more than it does BHC in direct sprays as well as in films, and the appropriate arrows have been drawn in Table IX.

(*d*) Further comparisons were attempted, but the evidence was found insufficient to justify them. In particular, there seemed no reason to suppose that PB synergised pyrethrins more intensely in the direct sprays than in the films. There may be a special reason for this, however. The concentrations of pyrethrins were of the same order in the direct spray tests as in the film, whereas those of DDT and BHC were necessarily made higher in the former to obtain interpretable data. All the mixtures contained DDT or BHC except those of pyrethrins with PB, and so the fact that the DDT and BHC concentrations differed between the films and direct sprays may be responsible, in some way not yet apparent, for the pairs containing DDT and/or BHC having higher joint toxicities as direct sprays than as films. If this is correct, the comparisons of the second type (between methods of application) are of minor importance, though the agreement in direction between them all (save one omission) is in a sense a corollary of the comparisons of the first type being parallel.

The comparisons of the first type (within methods of application) thus appear the more important. A simple convention helps to express succinctly those made in Tables VIII and IX. If A, B, and C are three materials, then let A[B>C] mean that the joint toxicity of a mixture containing A is lowered when the other constituent, B, is replaced by C, *i.e.*, A+B has a higher joint toxicity than A+C. The results then seem consistent, since in all probability for both films and direct sprays,

(i) Pyr.[PB, BHC>DDT],
(ii) PB [Pyr.>BHC>DDT],
(iii) DDT[Pyr.>PB],
(iv) DDT[BHC>PB].

From (ii) it is obvious that PB[Pyr.>DDT], though the same conclusion can be deduced from (i) and (iii). The absence of BHC outside the brackets in (i)–(iv) appears to be of no special significance. This consistency indicates that independent joint action is a relevant standard in considering the joint toxicities of mixtures of any two of these substances.

Summary.

The effect of piperonyl butoxide (PB) on the toxicities of allethrin, DDT, and BHC in a heavy oil base to *Tribolium castaneum* beetles has been tested. PB synergised allethrin and BHC both in films and direct sprays. It antagonized DDT in films, but left the toxicity of DDT unchanged in direct sprays.

The effect of PB on the joint toxicity of BHC and pyrethrins to *T. castaneum* was also investigated, applying the materials as direct sprays. The data were not so conclusive as had been hoped, but they indicated strongly that in a mixture containing all three materials the PB synergised each insecticide as though the other were absent, *i.e.*, it synergised both simultaneously.

The experimental findings of the present paper are examined in conjunction with the findings of Hewlett and Plackett (1950). It is shown that there is an underlying similarity between the film and direct spray results for the joint toxicities to *T. castaneum* of pyrethrins, DDT, BHC, and PB, taken in pairs.

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SOME OBSERVATIONS ON RESTING TSETSE-FLY POPULATIONS, AND EVIDENCE THAT *GLOSSINA MEDICORUM* IS A CARRIER OF TRYPANOSOMES.

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In a recent paper (Nash & Davey, 1950) it was pointed out that by examining the trunks of saplings and creeper stems, it is possible to find at rest certain species of tsetse which will not readily attack man. This paper describes some further observations upon *Glossina medicorum* Aust. and *G. fusca* (Wlk.), made with this technique in the forest belt, and also an attempt to adapt the method to the study of *G. morsitans* Westw. in the woodland savannah zone.

The normal methods used in studying tsetse-fly populations can be classified as " bait techniques ", the essential being that *active* flies are attracted to man, or bait-animals, or to inanimate objects such as traps, which by reason of shape, colour, contrasting light and shade, or scent, are attractive to the active tsetse which is searching either for food or for the opposite sex. Under this heading come human bait, cattle bait, trap bait and screen bait techniques.

In direct contrast to the above is the " resting-haunt technique " in which man searches for the *inactive* tsetse whilst it is at rest.

With those species of tsetse which are inactive during the day and feed at night, the resting-haunt technique should theoretically reveal the whole population of the area searched ; but with those species that are normally active in the day-time one cannot hope for such results, but one can hope to study that section of the population which is inactive, and which would therefore not appear with any of the bait techniques.

Observations on *G. medicorum* **and** *G. fusca.*

General.

The Olokemeji Forest Reserve, which was described in the previous paper, was again visited at the end of the rains. The main object was to train staff in the resting-haunt technique and to confirm and enlarge upon the observations made a year previously.

During 5½ collecting days, six fly boys caught a total of 200 *G. medicorum* and *G. fusca,* all of which were taken at rest on the trunks of saplings and the stems of creepers, and with their heads pointing downwards. Only one specimen would have been taken by the human bait technique, since, during the entire collecting period, only one fly came to man.

Of the total catch 62 per cent. were *G. medicorum,* and 38 per cent. *G. fusca. G. medicorum* appeared to be commoner in the forest nearer the Ogun river, and *G. fusca* in the forest further away from the river.

This technique of spotting resting tsetse naturally requires good eyesight, but of even greater importance is the collector's power of concentration which is dependent on sustained enthusiasm. A well-trained fly boy, who expects to have his wandering thoughts recalled by the distinctive pitch of an approaching *G. palpalis* (R.-D.) or *G. morsitans,* may be useless in this method of collecting. There would appear to be a great variation in the aptitude of the individual for this work. For example, out of six Africans all new to the technique, one man on the third day's training found 27 flies in one morning (5 F.B.H.), whilst the other five men could only find 40 between them (1·6 F.B.H.). The adept, although poorly educated, continued to be much better than his fellows during the ensuing days. This work imposes a great strain on both the eyes and the mind, so that an hour's search should be followed by half an hour's rest.

Out of 119 *G. medicorum*, 45 per cent. were females, and out of 73 *G. fusca*, 44 per cent. were females ; clearly this technique yields a good cross-section of the population.

According to the searchers, flies tended to be found nearer to ground-level as the day advanced ; possibly in the late dry season they settle on the forest floor.

Gorged flies, which were believed to have fed overnight, were exceedingly numerous. Out of 15 recently gorged *G. medicorum* and eight *G. fusca* examined, all were found to contain mammalian blood. Gorged flies were observed to be scarce on the morning after a night of rain, which is what might be expected if these species are nocturnal feeders.

Nocturnal activity.

Rather unsuccessful attempts were made to find out whether these tsetse engage in crepuscular or nocturnal activity. The first night catch was started before dawn, at 5.30 a.m. It was very dark under the trees and a torch had to be used whilst walking, but it was switched off during the frequent stops. Often a distinctive, droning whine was heard around the head, and then the noise receded, suggesting that a tsetse had investigated a possible host and had found it to be unattractive. Sometimes the noise would cease abruptly, as though the insect had stopped and settled. On one occasion the noise ceased very suddenly, and turning on his torch the writer saw a tsetse settled on a leaf, facing him, and within 18 inches of his chest. It proved to be a female *G. medicorum.*

When the light of the new day started to filter through the trees, the buzzes became rarer, and had ceased by 6.45 a.m. Unfortunately, on no other occasion were we able to catch the insect which produced this most characteristic tsetse-like noise, but if it be agreed from this slender evidence that this noise is produced by tsetse the following notes may be of interest.

26.x.50. 8.45–9.30 p.m. Moon full, but not high enough to illuminate more than the occasional open space in the forest. No buzzes heard.
9.30–10 p.m. Path fully illuminated by the moon. A few definite buzzes heard, but negligible in number compared to those heard in the pre-dawn catch.

27.x.50. 6.15–7.25 p.m. The sun set at 6.15 p.m., but there was twilight of decreasing intensity until about 7 p.m. The moon was not yet up. Many buzzes were heard from passing flies, but they took no interest in us with the exception of one large tsetse which settled on a man's exposed leg ; however, it flew off as soon as the torch was switched on. No more buzzes were heard after it became really dark at 7 p.m.

28.x.50. 6.15–7.20 p.m. It was rather darker than the previous night owing to cloud-bank in the west. A pure black goat and a blackish-brown sheep were added to the party. Only five buzzes were heard up till 7 p.m., after which there were no more. No tsetse were seen.

30.x.50. 5.30–6.50 a.m. There had been torrential rain earlier on in the night, so that the vegetation was very wet. A partially obscured moon gave a fair amount of light. Dawn came at about 6.10 a.m. Between 5.45 a.m. and 6.35 a.m., nine buzzes were heard.

Incomplete though these observations are, they suggest that at this season these tsetse may confine their feeding to the twilight hours or when the forest is fully illuminated by the moon. These characteristic buzzes were never heard in the forest during the daylight hours when tree trunks were being searched, and flies were found at rest.

Breeding grounds.

A morning's search by five men failed to produce any pupae in the classical tsetse-breeding sites. It is possible that the pupae of these species are scattered over the forest floor.

The effectiveness of the resting-haunt technique within natural forest.

As explained in the previous paper (Nash & Davey, 1950) this resting-haunt technique was developed in the somewhat unnatural vegetational conditions of a part of the forest reserve which was characterised by an understorey of saplings of introduced species of trees. Since it was desirable to investigate the effectiveness of the technique under normal conditions, a morning was spent on a high hill covered in natural forest overlooking the Ogun river.

An area was selected where the upper forest canopy was sufficiently developed to have reduced the undergrowth until it was fairly easily penetrable by man. This is an essential condition, as if one has to push one's way through undergrowth, one sets all the creepers in motion and disturbs the resting flies.

Nine men in 1½ hours caught 13 flies (1 F.B.H.) but our expert searcher took five of them. The catch consisted of 12 *G. fusca* and one *G. medicorum* ; out of eight female *G. fusca*, all were gorged with blood.

All the specimens were taken at about 7 feet above ground level and mostly off vertically hanging creeper stems, or thin saplings about 1 inch in diameter. Frequently, the presence of other creepers effectively protected the fly from the net ; thus in the first hour's catch we caught seven flies and missed eleven. On no occasion was a fly found resting on a horizontal creeper or bough, or on the trunk of a large tree.

Climate when the above observations were made.

Wet and dry bulb readings were taken with a whirling psychrometer when all the searches were made ; the mean figures for the various times of day can be summarised as follows.

Time of searches	Temp. °F.	R.H. %
Dawn searches 5.30–7 a.m. ...	72	90
Noon	84	70
Sunset searches 6.15–7 p.m. ...	80	85
Early night searches 9 p.m. ...	77	87

At this season the temperature ranged between 72 and 84°F. (22–29°C.), and the relative humidity between 70 and 90 per cent.

G. medicorum as a Carrier of Trypanosomes.

Up to three years ago, only one specimen of *G. medicorum* had ever been taken in Nigeria, and Vilain (1948) in his paper on the geographical distribution of tsetse in French West Africa refers to it as a rare species. But the application of the resting-haunt technique to other areas may show that in reality this species is widely distributed, in which case it might be of considerable economic importance. The following evidence shows that *G. medicorum* is potentially a dangerous species.

No difficulty was found in collecting 50 specimens by the resting-haunt technique. These were dissected, and revealed a mature trypanosome infection rate of 14 per cent. Details are given in Table I.

TABLE I.

Trypanosome infection rate amongst *G. medicorum.*

G. medicorum ...	Trypanosomes in salivary glands	Trypanosomes in hypopharynx only	Trypanosomes in hypopharynx and gut.
	brucei Group	*vivax* Group	*congolense* Group
29 ♂♂	0	3	1
21 ♀♀	0	0	3
50 flies	0 flies	3 flies	4 flies

G. medicorum shows almost no interest in man as a host and is therefore unlikely to be of any medical consequence, but the above results indicate that it is a vector of trypanosomes of both the *vivax* and *congolense* groups and is therefore likely to be of veterinary importance. There is plenty of grassland adjacent to the Olokemeji forests where cattle could probably be kept, were it not for the presence of tsetse.

Even though the observations made in the late rains suggest that *G. medicorum* is nocturnal in habit and would therefore only attack cattle in their kraals at night, future research may well show that during the hot, dry weather hunger may force this tsetse to attack preferred hosts in the day-time, as does *G. fusca.*

The most likely natural hosts, and trypanosome reservoirs, for *G. medicorum* are harnessed antelope (*Tragelaphus scriptus*) and duiker (*Cephalophus* sp.), which were stated by the Forest Guard to be numerous in the localities in which this species was found. Since the resting-haunt technique yields such large numbers of recently gorged specimens, it should be possible to ascertain the wild hosts by the precipitin test.

Observations on *G. morsitans.*

An attempt was made to apply the resting-haunt technique to *G. morsitans* in a fly-belt some 30 miles north-east of Kaduna, northern Nigeria, where the vegetation is typical *Isoberlinia doka* woodland.

Searching the resting haunts, without the aid of cattle.

In November 1950, nine days were spent in searching trees for *G. morsitans,* but since only 14 flies were taken the method was abandoned.

The main trouble was that many of the flies were resting far above the reach of the catcher, some being as much as 14 feet above ground level ; *G. morsitans* is much more alert than the forest species, so that clumsy methods of catching them, such as one man standing on another man's shoulders, were usually unsuccessful. Even when flies were resting within reach, the presence of dry grass, at that season, prevented a sufficiently cautious approach.

Although so few tsetse were caught some interesting observations were made. The 14 specimens found were resting on the under side of more or less horizontal boughs, dorsum downwards, and usually some 9 feet above ground-level. The species of tree seemed to be of no importance *per se,* but *Cussonia nigerica* was much favoured, probably because the branches of this species frequently grow out horizontally.

Out of the 14 flies caught, 71 per cent. were females, 72 per cent. were in the intermediate hunger stage, and 100 per cent. were resting upside-down with the dorsum facing the ground.

Searching the resting haunts with the aid of cattle.

The whole purpose of the investigation was to study inactive tsetse which were at rest, but with *G. morsitans* there was always the probability that active flies attracted by man would settle on a tree beside the catcher and be caught ; these would then be erroneously included in the figures for inactive, resting tsetse. It was felt that this source of error, due to the attractive influence of the three searchers, could only be excluded by introducing a much more favoured host in the form of a herd of cattle. By using the resting-haunt technique in the presence of cattle one should get a cross-section of the inactive fly population, such as might be found after the passage of game.

When searching for resting tsetse in the presence of cattle it was observed that *G. morsitans* never came to man, and that few could be seen on the moving animals, although, judging by the number of gorged flies found on the trees, tsetse must have been very numerous. On one occasion we had our breakfast with the herd around us and never saw a tsetse, and yet by the end of the meal the searchers had found a dozen gorged flies.

(*a*) *Components of the tsetse population.*

A comparison was made of the components of the tsetse population as revealed by the human bait technique, with those found by the resting-haunt technique in the presence of cattle.

The method employed was for the searchers to examine trees for half an hour in the presence of cattle, then to walk for five minutes away into the woodland, and finally to do an ordinary half-hour catch of tsetse attracted to man. The work started at 8 a.m. and finished at 11.25 a.m., enabling three catches to be made by each method. The data were collected in January and February, that is in the mid-dry season, and after the grass had been burnt.

The hunger staging was rather crudely done by the writer's simplification of Dr. C. H. N. Jackson's method (Nash, 1937). Since the same assistant did the hunger staging throughout, the standard should have remained constant ; possibly some of the less obviously starved flies should really have been included in the intermediate group. A fly is classed as gorged when the centre of the abdomen is red or black with ingested blood ; if only the sternites appear black, then the fly is graded

TABLE II.

Comparison of the components of a *G. morsitans* population attracted to man, with those of a population found on trees in the presence of grazing cattle.

Flies caught, having been *attracted by* Man

Total caught	Females %	Young flies %	Gorged flies %	Intermediate flies %	Starved flies %
897	21	18	15	46	38

Flies *found on Trees* amid grazing Cattle

Total caught	Females %	Young flies %	Gorged flies %	Intermediate flies %	Starved flies %
826	40	5	69	24	7

as intermediate. It was essential to make the experiment simple, as the assistant in charge, although absolutely reliable, was not capable of coping with anything complicated.

A comparison of the two lots of figures obtained by the two different methods is given in Table II.

The percentage of females attracted to man was unusually high suggesting that the flies were hungry, an observation which is confirmed by the high percentage of starved flies, and the scarcity of game.

The percentage of females taken off trees in the vicinity of the cattle was almost twice as great, which was only to be expected as it is well known that the females of this species do not normally appear to man in their true numbers. Likewise, the very large percentage of gorged flies was to be expected, as most of these had just left the cattle ; but the fact that almost one-third of the catch was not gorged suggests that this proportion of the catch consisted of flies that were already at rest on the trees.

(*b*) *Average resting height in relation to the hunger stage.*

The approximate height above ground level at which each resting fly was found was recorded, together with other data for each individual fly. There appears to be no relationship between sex and resting height, but a marked relationship between hunger stage and resting height. The average resting height was worked out for all individuals in each hunger stage group, giving the following results.

The average resting height amongst 526 gorged flies was 2·9 ft. (0·88 m.)
,, ,, ,, ,, ,, 196 intermediate flies was 5·9 ft. (1·80 m.)
,, ,, ,, ,, ,, 56 starved flies was 6·1 ft. (1·86 m.)

The results suggest that tsetse from the intermediate and starved groups rest at twice the height of those from the gorged group ; actually the difference is believed to be much greater, as many flies from the higher resting groups are missed, and many more are inaccessible. Flies have been seen at rest at heights estimated by the writer to be as much as 14 feet (4·3 m.).

The figures given above are average heights, but there is a considerable range amongst individuals of the same group, a few settling much higher than the average figure and a few much lower.

(*c*) *Resting position in relation to the hunger stage.*

In addition to the observations already mentioned, notes were made of the resting position adopted by each fly.

G. morsitans may be found resting on tree trunks in a vertical position with the head facing either upwards or downwards, or they may be found resting on the under side of branches in a horizontal position with the dorsum facing downwards.

The distribution of resting positions amongst the total catch of 783 flies is given below.

Position	Percentage found in that position
Vertical, head downwards	2
Vertical, head upwards	62
Horizontal, dorsum downwards ...	35

Clearly the majority of the flies were resting head upwards in the vertical plane, but about one-third were resting dorsum downwards in the horizontal plane.

In order to discover the reason for this, the crude data were further analysed. There appears to be no relationship between resting position and sex, as will be demonstrated later, but there is evidently a close relationship between the hunger stage and the position adopted by the resting fly (Table III).

TABLE III.

The resting positions of 783 *G. morsitans* according to the hunger stage.

Hunger stage	Total flies observed	Percentage of flies observed in different resting positions		
		Vertical : head downwards	Vertical : head upwards	Horizontal : dorsum downwards
Gorged	532	1	80	19
Intermediate ...	195	4	24	72
Starved	56	7	27	66

Clearly gorged flies rest mainly on vertical surfaces with their heads pointing upwards, whereas intermediate and starved flies prefer to rest in the horizontal plane, with the dorsal surface facing downwards. Very few flies of this species rest head downwards.

It is suggested that the recently fed fly settles head upwards on the tree trunk so that the drops of exudate shall not foul the tip of the abdomen ; when this stage in the digestion of the meal is over, the tsetse, which is now much lighter, tends to select a higher and presumably safer position, and hangs upside down on a horizontal branch, from which it will get a much wider field of vision ; this will be an advantage both for self-protection, and for detecting a potential host when the insect again feels hungry.

These results are very different from those found for *G. fusca* and *G. medicorum* which rest head downwards ; unfortunately no hunger staging was done for these species owing to the brief time available. It is worth pointing out, however, that these tsetse with their very long fore-legs are really resting at an angle of about 45 degrees from the bark and that consequently drops of exudate would be far less likely to foul the abdomen or legs.

A comparison of the results obtained from the initial tree trunk searches without cattle with those in which cattle were employed, shows that, using the former method

TABLE IV.

The percentage of females in relation to the resting position and the hunger stage.

Resting position	Total flies	♀ %	Hunger stage	Total flies	♀ %
Vertical :— Head upwards ...	489	43	Gorged	532	40
Horizontal :— Dorsum downwards	277	32	Intermediate ...	195	37
Vertical :— Head downwards ...	17	18	Starved	56	25

we were only getting those flies in which digestion was well advanced, *i.e.*, flies resting horizontally at high levels, and in the intermediate hunger stage ; the dry grass was still unburnt in many places, so that the more recently fed flies, which would have been resting at low levels, would have flown off before the searcher could have seen them. It would seem that if a true cross-section of the inactive population is to be obtained, tree searching must be carried out after the fires, or whilst the new grass is still short, and that some method of catching the high-resting flies must be found.

(*d*) *Resting position in relation to sex.*

The results given in the first three columns of Table IV at first sight suggest that the sexes may adopt rather different resting positions ; however, such differences are believed to be related to the hunger stage, rather than to sex *per se*. In the last three columns of Table IV the sex proportion is shown for the flies in each hunger stage. It will be remembered from Table III that the bulk of the flies resting head upwards were gorged, and it will be seen from Table IV that the female percentage amongst " Head upwards " and " Gorged " flies is very similar ; this approximate agreement holds good for the other two resting positions and hunger stages. All that can be said is that among the few flies resting head downwards, the majority are starved males.

It might be expected that when using the resting-haunt technique one would catch the sexes in equal proportions, but as will be seen from Table II the female percentage for the total of resting flies caught was only 40 per cent. In an attempt to find an explanation for this lower percentage of females, the sex proportions was analysed for flies found at heights of 6 feet or over, but this gave a female percentage of only 34 per cent. At this season, breeding is confined to the evergreen vegetation bordering streams ; a certain proportion of the female population must always be visiting the breeding grounds, so this may account for the smaller proportion of females in the main woodland block where the experiments were carried out.

(*e*) *Additional investigation carried out in the late dry season.*

The experiment carried out in January and February was repeated during the latter half of March 1951, in order to check whether the results already obtained were applicable to the much hotter weather. The only difference was that flies had become considerably hungrier : thus out of a further 504 flies taken by the human bait technique it was found that the percentage of starved flies had risen from 38 to 48 per cent., and that the percentage of gorged flies had fallen from 15 to 9 per cent.

This increase in hunger was strongly reflected in the results obtained by the resting-haunt technique in the presence of cattle. Thus out of a further 390 flies taken at rest, the percentage of gorged flies had risen from 69 to 94 per cent., suggesting that under these severe climatic conditions very few of the flies present had failed to take a meal.

Out of 366 gorged flies, 84 per cent. were resting head upwards in the vertical plane as against 80 per cent. in the previous experiments (Table III). The average resting height of the gorged flies had risen slightly from 2·9 to 3·2 ft. Since only 24 intermediate and starved flies were taken at rest, the numbers were too few to give any valid results as to resting height or position for these hunger stages.

Summary.

Further studies were made of *G. medicorum* and *G. fusca* using the resting-haunt technique.

During 5½ collecting days, 200 *G. medicorum* and *G. fusca* were taken by the resting-haunt technique ; over this period, only one fly was taken by the normal, human bait technique.

Out of 119 *G. medicorum* 45 per cent. were females, and out of 73 *G. fusca*, 44 per cent. were females ; the resting-haunt technique yields a good cross-section of the tsetse population.

Out of 15 recently gorged *G. medicorum* and eight *G. fusca* examined, all contained mammalian blood. Gorged flies were very numerous, so that it should be possible to ascertain the wild hosts by the precipitin test.

From the evidence available, it is believed that at the end of the rains both *G. medicorum* and *G. fusca* feed only during the twilight hours, or when the forest is fully illuminated by the moon.

The resting-haunt technique was developed in unnatural forest characterised by an under-storey of saplings of introduced species of trees ; however, the technique has now been satisfactorily tested in natural forest, and is effective, providing forest is selected in which the undergrowth has been sufficiently suppressed, by an adequate canopy, to make quiet access possible. The majority of the flies were found resting on vertically hanging creeper stems, or thin saplings about one inch in diameter.

Out of 50 *G. medicorum* dissected, 14 per cent. showed mature trypanosome infections. It would appear therefore that *G. medicorum* is potentially of economic importance.

An attempt was made to apply the resting-haunt technique to *G. morsitans*.

A comparison of catches of flies attracted to man with those taken off trees, in the presence of cattle, showed that by using the latter method the catch of females could be doubled ; further, since about one-third of the flies found at rest were not gorged, this proportion of the catch must have already been at rest on the trees.

Whereas the average height at which gorged flies rest is only 3 ft. (0·9 metres) above ground level, the average height at which intermediate and starved flies rest is certainly 6 ft. (1·8 metres), and probably very much more. Flies have often been seen resting at about 14 ft. (4·3 metres) above ground-level, a fact which should be taken into account when using insecticides from the ground.

The majority of gorged flies rest on tree-trunks in the vertical plane with the head upwards—a posture which should prevent the abdomen from becoming fouled with drops of exudate.

The majority of intermediate and starved flies rest on the under-side of horizontal branches with the dorsum downwards, which should give them some protection from the aerial spraying or dusting of insecticides.

Only a very few flies rest in the vertical plane with the head downwards ; the bulk of such flies are very hungry males.

It appears that after the early stages of digestion are complete, and the tsetse has lightened itself appreciably by exuding much of the liquid content of the meal, the insect probably selects a higher resting position ; here, hanging upside down, it will greatly increase its field of vision and hence be safer from predators, and be in a better position to see passing hosts when it becomes hungry.

Acknowledgements.

For help in obtaining the data quoted in the first part of this paper, dealing with *G. fusca* and *G. medicorum*, I am indebted to Mr. A. H. Parker, Entomologist, West African Institute for Trypanosomiasis Research, who accompanied me, and took part in the investigation. I am also indebted to Col. H. W. Mulligan, Director, for his valuable criticism of the manuscript.

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THE COLLECTION OF THE CACTUS WEEVIL, *CACTOPHAGUS SPINOLAE* (GYLH.), IN MEXICO AND ITS DISPATCH TO SOUTH AFRICA.

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Commonwealth Institute of Biological Control.

The Division of Entomology of the Department of Agriculture of the Union of South Africa has for a number of years been interested in obtaining the cactus weevil, *Cactophagus spinolae* (Gylh.), to supplement the biological control of *Opuntia megacantha* and *O. aurantiaca.* The other two species of prickly-pear involved, *O. inermis* and *O. stricta,* are relatively unimportant in South Africa.

Prior to 1945, attempts, mainly by the Commonwealth Institute of Entomology through correspondence, to make arrangements to obtain this weevil from Mexico were unsuccessful. In 1945, the Commonwealth Bureau of Biological Control was asked to collect 2,000 living specimens of it for dispatch to South Africa. Negotiations by Dr. W. R. Thompson, Director of the Bureau, with the Entomological Laboratory of the United States Department of Agriculture in Mexico City, and by W. F. Sellers with the Direccion General de Agricultura and the Oficina Fitosanitaria Investigación y Divulgación, Mexico, D.F., were inconclusive. In 1946, it became evident that the only practical way to obtain this weevil in quantity was for the writer to go to Mexico City. This resulted in the collection and dispatch of 862 adults in 1946, 1,396 in 1947 and 15,584 in 1948 to meet the requirements of South Africa.

This paper summarises the available information relating to the ecology, distribution and food preferences of *Cactophagus spinolae,* and also records the results of collecting it in Mexico and the development of a suitable container for transporting it by air. Apart from the advice furnished by the Mexican Department of Agriculture on the distribution and monthly occurrence of the weevil, practically all the background information is taken from the published results of the Australian foreign exploration investigations arising from the biological-control campaign against the prickly-pear in Australia. In 1948, Alan P. Dodd, Director of the Biological Section, Department of Public Lands, Brisbane, Australia, furnished considerable specific information on the distribution and occurrence of this weevil.

The *Cactophagus* weevils, which belong to the subfamily Calandrinae, are the most destructive cactus insects in Mexico. *Cactophagus spinolae* (figs. 1 & 2), the most destructive species, is a large black insect with distinctive red markings. There are three other related species that attack plants of the genera *Platyopuntia, Nopalea* and *Cereus,* either in Mexico or Central America. *C. validus* (Lec.) is a west-coast species common in the State of Sinaloa where it is very injurious to prickly-pear of the shrub type ; it has been recorded as far north as Arizona and California. *C. fåhraei* (Gylh.) and *C. striatoforatus* (Gylh.) are destructive to prickly-pear of the tree type and to *Cereus,* the former in southern Mexico and the latter in Salvador and Guatemala in Central America ; *C. striatoforatus* has also been recorded from Trinidad.

Opuntia (

The known distribution of *Cactophagus spinolae* is central Mexico, from the southern edge of the States of Chihuahua and Tamaulipas in the north to as far south as the States of Guerrero, Puebla, and Veracruz.

Adult emergence occurs shortly after the end of the dry winter season. The Mexican Department of Agriculture indicates that the best time to collect beetles is in the months of April, May and June in the Federal District and the State of Mexico, and August and September in the States of Jalisco, Guanajuato, Michoacan, Morelos,

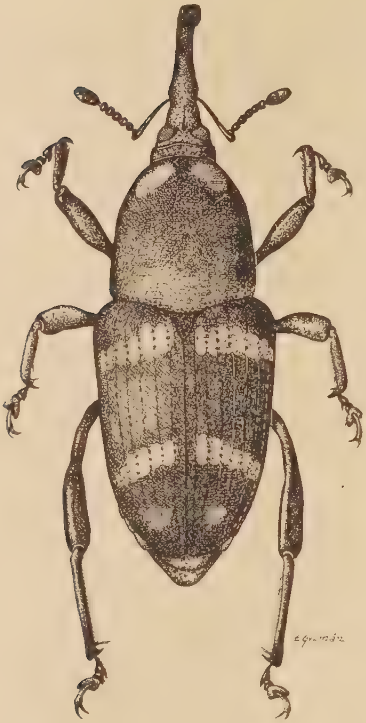

Fig. 1.—*C. spinolae* (Gylh.). Dorsal view of adult.

Guerrero and Veracruz. A. P. Dodd indicates the common occurrence of adults from May to September, and his records add the States of Chihuahua, Durango, Zacatecas, Aguascalientes, San Luis Potosi, Tamaulipas, Tlaxcala, and Puebla. The best time for large-scale collecting in the Tlaxcala-Puebla area and in parts of the States of Morelos and Mexico is between May and August.

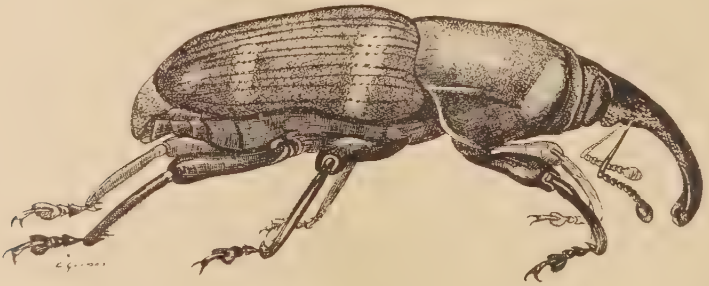

Fig. 2.—*C. spinolae* (Gylh.). Lateral view of adult.

There appears to be one generation a year. The duration of adult life varies from several months to over a year. The adults feed, principally at night, on the tender

AUSTRALIAN FOOD PLANT TESTS.

PLANTS ON WHICH FEEDING AND DEVELOPMENT OCCURRED.
(Information extracted from *The Biological Campaign against Prickly-pear* by A. P. Dodd, Brisbane, 1940.)

Plant	Adults	Oviposition	Larvae
Banana. Cages surrounding lower and upper parts of plants	Punctured stems and midribs of leaves causing minor injury	None	—
Banana fruit.* Caged fruit	Fed on flower sheaths, very young fruit and large green fruit; survived 7 months	Less than one egg per ♀ in partially-eaten fruit	Fed on pulp and fruit damaged by adults; produced normal adults when fed on fruit in contact.
Uninjured green fruit	—	—	Newly hatched larvae did not feed.
Ripening fruit ...	—	—	Newly hatched larvae developed on fruit in contact, pupating in from 60 to 105 days.
Pumpkin fruit... ...	Fed freely on picked fruit	Several eggs ...	Young larvae did not survive.
Pawpaw stems ...	No feeding ...	None	Developing larvae tunnelled freely. Majority died in 30 days; one pupated in 62 days and produced small adult. Newly hatched larvae did not feed.
Picked ripened fruit	Fed to some extent	None	Newly hatched larvae did not feed.
Tomato stems... ...	—	—	One small larva survived 70 days; one-third grown at death.
Maize stems	Punctured and injured stems of large plants	None	Newly hatched larvae did not survive.

*In preference tests with a choice of banana fruit and prickly-pear, the adults fed exclusively upon prickly-pear, and oviposition occurred normally in it. This choice should be compared with the development in tests on banana fruit under unnatural conditions. The evidence from field surveys in Mexico definitely indicated that *C. spinolae* is restricted to cactus plants in its natural choice of food, even when grown in close proximity to bananas.

shoots, fruits, and pads, but can survive several weeks without food. The larvae live in the segments and stems of species of *Platyopuntia*, tunnelling from joint to joint, and frequently destroy whole plants by causing weakening and disintegration of the stems and branches, and conditions favourable for decay of the tissues. When fully grown, the larva is about one inch in length. Pupation takes place in the hollow stems of the plant. In areas where the prickly-pears are grown as a crop for food, hand-picking of the adult beetles is frequently undertaken to lessen the damage.

The Australian authorities decided not to liberate *Cactophagus spinolae* against prickly-pear in Australia. The results of their food-plant and starvation tests, while not entirely favourable or satisfactory, were not the only reason for this ; another reason apparently was that certain related insects, notably the sugar-cane weevil *Rhabdoscelus* (*Rhabdocnemis*) *obscurus* (Boisd.), and the banana weevil, *Cosmopolites sordidus* (Germ.), were recognized as serious pests and were known to be difficult to control. Adults of *Cactophagus spinolae* were tested for feeding, longevity and oviposition ; they fed on pumpkin fruit, banana fruit and maize stems. Larvae fed on tomato stems, pawpaw stems and banana fruit. The results of these tests were considered unsatisfactory because of feeding (and also oviposition) on plants other than prickly-pear, and it was consequently felt that the liberation of *C. spinolae* in Australia was undesirable. Because of this decision, the related species, *C. validus*, *C. fåhraei* and *C. striatoforatus* were not tested. However, the Australian entomologists did demonstrate more or less conclusively that, as far as the natural choice of food plants is concerned, *C. spinolae* is unlikely to persist on plants other than prickly-pear and *Cereus*.

The decision to introduce *Cactophagus spinolae* into the Union of South Africa makes it desirable that food-plant and starvation tests should be conducted with the other three species, *C. validus*, *C. fåhraei* and *C. striatoforatus*, which might be useful in the general campaign against the prickly-pear.

The 1946 Collections.

On the 9th July the Mexican Department of Agriculture telegraphed that collections of *Cactophagus spinolae* could be made. The locating and surveying of suitable places started on the 19th July.

Accompanied by J. G. Shaw of the United States Laboratory, Mexico City, the writer first located the weevil on the 22nd July at San Andrés a few miles south of Mexico City at an elevation of 2,500 metres. During the following week, a number of places were visited at this approximate elevation in the environs of Mexico City in the District Federal and the State of Mexico. The majority of the beetles obtained were collected at San Andrés, D.F., but some numbers were collected on the south-east road to Amecameca (2,532 m.), at Tlalpizahua (2,248 m.), Ayotala (2,247 m.) and Tlalmanalco (2,328 m.), all in the State of Mexico. Beetles were not found in Chalco (2,280 m.), Mexico, north of Tlalpizahua, the best collecting place in this area. A few were obtained at San Angel, Tetelpan, D.F. (2,469 m.) ; San Angel is north and slightly west of San Andrés. None was found at Toluca (2,680 m.), Mexico.

Between the 22nd and 31st July, 864 beetles were collected ; the largest collection being 266 on the 26th. The sexes appeared to be represented equally, and the collections apparently comprised the most recently emerged beetles in this general area. In any particular locality, the weevils were obtained fairly readily on the first trip to any particular locality, stragglers were collected on the second and third trips, and practically nothing on the later trips. At this time of year and at the elevations indicated above, the weevil was present on the spineless cactus and practically non-existent on the spined varieties.

A consignment comprising 400 beetles was dispatched from Mexico City on the 27th July 1946, and another, of 462, on the 1st August 1946, both by Pan American Airways to Montreal, Canada. British Overseas Airways Corporation transported the consignments from Montreal to Johannesburg via London. On the 26th August, Dr. T. J. Naudé, Chief of the Division of Entomology, Pretoria, South Africa, cabled that the insects had arrived in excellent condition.

The 1947 Collections.

Due to circumstances beyond control, collecting in 1947 was not begun until the 12th August. Despite the late start, 1,415 adults were collected in the vicinity of Mexico City between the 13th and 27th August. Seven hundred and three weevils were collected at San Andrés and 675 at San Angel, the largest collection being 376 on the 18th. The others were collected at Tlalpizahua (26), Tlalmanalco (10), and Ayotla (1).

The size of the collections at this late date is considered to be the result of an unforeseen development. Large numbers of weevils appeared immediately after two hurricanes that occurred during the week of the 10th to 16th August. The insect became scarce again a few days later. Observations in 1946 indicated that the period during which the collections were made was the season of heavy mating following complete emergence. In 1947, the collections were made after the season of optimum mating, and females seemed to predominate.

The damage to the cactus plants at San Andrés and San Angel appeared to be more severe in 1947 than in 1946. Apart from the hurricane disturbance, the larger collections may have been due in part to the familiarity of the collectors with the weevil and the larger area over which the search was made. One woman at San Andrés stated that she had destroyed many weevils that she found in her garden at an earlier date, and the collectors at San Angel thought that the insect had been more abundant earlier in the season.

C. spinolae unexpectedly became scarce at San Andrés and San Angel after the 18th August. Attempts to organise collecting at Tlalpizahua, Ayotla and Tlalmanalco from the 22nd August were equally disappointing. These areas had yielded satisfactory numbers in 1946, and they would probably have done so in 1947 if they had been searched immediately after the hurricanes. A collector at Tlalpizahua stated that the weevils had been quite abundant earlier in the season.

In 1947, 1,396 weevils were sent in three consignments to South Africa. The first consignment, which consisted of 600 beetles, left Mexico City on the 19th August by air express and was carried by Pan American Airways to New York and by B.O.A.C. thence to Johannesburg via London. A second consignment comprised 618 beetles and left on 22nd August, and a third, of 178 beetles, left on 28th August, both by Pan American Airways from Mexico City to Johannesburg via Houston, Texas, and New York. Dr. Naudé reported that these consignments also arrived in excellent condition.

The 1948 Collections.

The experience gained in 1946 and 1947 indicated that if the weevil was to be obtained in larger numbers, new and larger areas should be explored and the collecting work started early in June.

A. P. Dodd reported that Tlaxcalancingo near Puebla had been a good collecting area in June, 1927. In 1948, this area yielded outstanding results ; 20,665 adults were collected between the 8th June and the 31st July, the largest collection being 4,296 on 30th June. A few of the earlier collections in 1948 were made at Penõ Pobre, La Fama, Las Fuentes and Santa Ursula, in the vicinity of Tlalpan, but these localities yielded only a few hundred beetles.

Five consignments were sent to South Africa in 1948, destined for Uitenhage ; they were dispatched by air express and were carried by Pan American Airways from Mexico to Johannesburg via New York. The results are tabulated on p. 48.

The boxes used for the first two consignments contained 500 beetles each, and those used for the other three contained 200 each. If the transit conditions of the various

Date of Departure	Date of Arrival	Days in Transit	Number of Weevils	Percentage Survival
26th June	10th July	14	5,000	67·8
3rd July	15th July	12	4,584	83·1
27th July*	7th August?	11 ?	2,000	93·3 ?
29th July*	7th August	9	2,000	93·3
2nd August	16th August	14	2,000	87·4

*As notification of arrival was received of only two of the last three consignments, it is assumed that these two consignments arrived together.

consignments are assumed to be similar, it must be concluded that the percentage of survival was higher when the transit time was of shorter duration and the boxes were less crowded.

Conditions in Transit.

The survival of insects transported by air is affected by various factors in addition to speed of travel and degree of crowding. If suitable arrangements are made, the harmful effects which would otherwise result from the conditions prevailing in transit can be avoided. The temperature in aircraft, both in flight and on the ground, is of great importance ; in winter, insect material is repeatedly lost by freezing, and in summer, it is exposed to alternating high and low temperatures with unfavourably high temperatures at tropical stops. Air pressure is also important, and the low pressures of high-altitude flying should be avoided.

It is particularly necessary to ensure that living insects are not placed in cargo holds that are neither air-conditioned nor pressurised. Some air carriers provide a restricted amount of cargo space with a temperature of 50°F. and pressurised for high-altitude flying at the barometric value normal for an altitude of 8,000 ft. If these or similar facilities are not provided, arrangements should be made to carry the consignment in one of the cabin compartments. As the air-conditioning does not operate at stops, some provision should be made to take care of the insects when the aircraft is on the ground if there is any danger of unfavourably high or low temperatures developing. All routes, compatible with fast transit time, that tend to favour the optimum conditions required should receive careful consideration before one is selected.

In 1946, 1947 and 1948, arrangements for the material of *C. spinolae* to be suitably and expeditiously tended were made only at Houston, Montreal and New York. Further experience has revealed that arrangements may be made with certain of the air carriers for consignments to be carried under cabin or passenger conditions, for special handling at transfer points to save time, for precautions to be taken to avoid exposure to abnormally high temperatures at tropical stop-overs, and for the avoidance of exposure to quarantine fumigation and insecticide-application practices.

The available information concerning the transit conditions for the three years is inadequate. In 1946, with 200 beetles per box, and in 1947, with 300, the consignments arrived in excellent condition. In 1948, the first consignment was held under the least favourable conditions before dispatch. The percentage of survival in the 1948 consignments seems to have been influenced by transit conditions and by some overcrowding in the case of the first two consignments. It is interesting to note that in the report on the Australian shipment from Mexico that arrived in Australia in July 1927, it is stated that of 4,000 weevils shipped, 3,562 or 89·1 per cent. survived the boat journey of several weeks.

Containers.

Each container (fig. 3) consists of a wooden sleeve of $\frac{3}{8}$-in. planed white pine with inside dimensions of 10 × 10 × 10 ins., the corner joints being rabbeted, glued and nailed. A partition of $\frac{3}{8}$ or $\frac{1}{2}$-in. hardware cloth is fastened 3 ins. from the bottom ; this partition is notched on one side to allow space for an eight-ounce, flat-sided, glass water bottle equipped with a rolled cotton wick, and the bottle is fixed in position with one strand of soft wire around the base and another around the narrow neck. The inner surfaces of the upper 7 ins. of the box are lined with wire netting to facilitate free movement of the beetles. The lower part of the box, below the cloth partition, is filled with a damp mixture of peat and sphagnum moss and is closed with a sheet of galvanised iron which forms the bottom of the box and is fixed in position with brads ; a few fine holes are punched in the bottom to provide emergency drainage. A pad of succulent cactus is wedged from corner to corner in the upper portion of the box, and a few loose strands of excelsior are placed on each side of the pad. A piece of brass-wire screen, 50-mesh or finer, is fastened across the top with tacks ; one corner is left unfastened until the beetles are counted into the box.

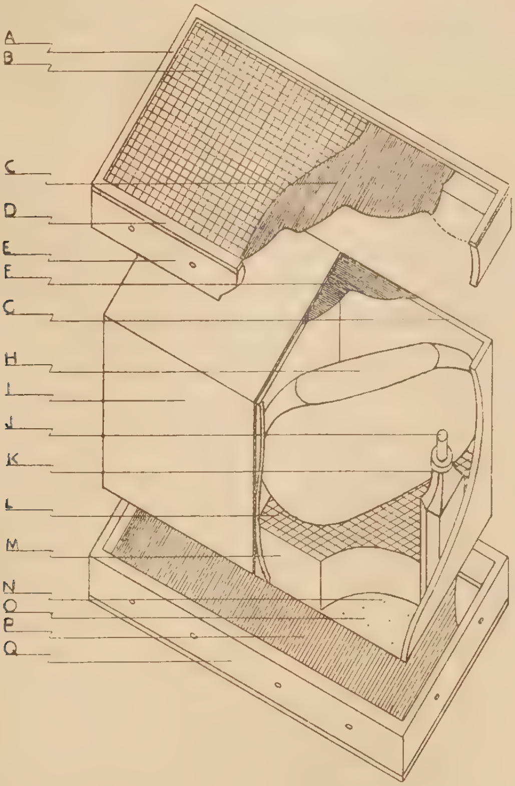

Fig. 3.—Container.(A) $\frac{1}{4}$ × $\frac{5}{8}$ in. moulding. (B) $\frac{1}{4}$ in. hardware cloth. (C) $\frac{1}{16}$ in. screen wire. (D) Top frame. (E) $\frac{1}{4}$ in. holes for retaining screws. (F) 50–90 mesh brass screen. (G) $\frac{3}{8}$ in. planed white pine. (H) Cactus pad. (I) Exterior of shipping box. (J) Cotton wick. (K) 8 oz. bottle (narrow neck, one flat side). (L) $\frac{1}{2}$–$\frac{5}{8}$ in. hardware cloth. (M) Mixture spanish moss and peat moss. (N) Galvanised sheet iron. (O) $\frac{1}{32}$ in. holes. (P) $\frac{1}{16}$ in. screen wire. (Q) Bottom frame.

NOTE.—Top and bottom frames constructed from $\frac{5}{8}$ × $2\frac{1}{4}$ ins. stock.

The boxes are shipped in pairs, those of each pair being held together by two wooden frames. The frames fit closely over and around the top and bottom of the pair and serve to provide additional strength, rigidity and protection. The frames are made from $\frac{5}{8}$-in. stock and are $2\frac{1}{4}$ ins. high ; ordinary house screen is fastened to each by $\frac{1}{4} \times \frac{5}{8}$-in. beading which gives an over-all height of $2\frac{1}{2}$ ins. The top frame is usually covered with $\frac{1}{4}$-in. hardware cloth as well as wire screen to give added protection to the brass screen in transit. The frames are fastened to the boxes by wood screws, usually two screws for each exposed side of each box of a pair. The wire screen netting is separated from the galvanised bottom and the brass-screen top by $\frac{3}{8}$-in. wooden stripping that is nailed round the inner surface of each frame just under the screen.

The boxes were stocked with fully fed beetles and assembled just prior to dispatch. The damp peat and sphagnum and the bottle provided sufficient moisture.

In 1945, a variation of this container was used for the forwarding by air of *Scolia ruficornis* F. from California to Western Samoa via Hawaii.

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The results of an undertaking of this sort are materially affected by the assistance and suggestions received from the entomologists, other scientists, and officials of the various countries concerned. It is impossible to mention everyone who actively co-operated. The writer wishes, however, particularly to thank those named below.

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Special thanks are due to Tito E. Rodriguez (1947) and Rogelio Rodriguez (1948) of C. Valles, S. L. P., for the efficient assistance received in making and dispatching the collections. Appreciation is expressed to Sr. E. Guzmán of the Oficina Fitosanitaria for the drawings of the adult *Cactophagus spinolae* and to G. G. Robinson of the Fontana Laboratory for the drawing of the container with cut-a-way sections.

Summary.

Collections of *Cactophagus spinolae* (Gylh.) were made in Mexico in 1946, 1947, and 1948 to supplement the biological control of prickly pear (*Opuntia* spp.) in South Africa. During these three years, 862, 1,396, and 15,584 adults, respectively, were dispatched to South Africa. The weevils were sent by air express in specially designed containers, and arrived in excellent condition.

This paper includes information on the distribution, life history and food preferences of *C. spinolae*. The need is stressed for anticipating the effects of transit conditions upon living insect material transported by aircraft.

A BHC-RESISTANT TICK.

By A. B. M. Whitnall, M.Sc., J. A. Thorburn, B.V.Sc., W. M. McHardy, B.Sc., B.V.Sc., G. B. Whitehead, M.Sc., and F. Meerholz.

(Plate IV.)

An arsenic-resistant strain of the one host blue tick, *Boophilus decoloratus* (Koch), was first noted in the East London district of South Africa in 1938–39 (du Toit, Graf & Bekker, 1941). Further evidence of this resistance and information concerning the spread of the tick were furnished by Omer-Cooper and Whitnall (1945). Investigations by Thorburn (1947), and by Whitnall and Bradford (1947, 1949), showed that the gamma isomer of benzene hexachloride (BHC) was extremely toxic to the arsenic-resistant tick. Early in 1946 " Gammexane " dips were in general use and in large areas of the Eastern Cape, Natal, Zululand and Swaziland they safeguarded the cattle industry.

These results were obtained with dip-washes containing 50 parts per million (p.p.m.) gamma isomer and, although some complaints were voiced about the ineffectiveness of this concentration of the dips against the three host bont tick, *Amblyomma hebraeum* Koch, no evidence could at first be found to show that they were ineffective against the one host arsenic-resistant blue tick, for which they were primarily recommended. However, in March 1948, it was observed that BHC dips failed to control blue ticks on three farms in the East London district. Then in December 1948, during the course of experiments in the Bathurst district, it was noted that, while the bont tick was controlled by 100 p.p.m. gamma isomer (Whitnall & others, 1951), the dips and sprays were ineffective against the blue tick.

The laboratory and field experiments discussed in this paper show that blue ticks from certain localities in the East London and Bathurst districts have developed a resistance to BHC and, at the same time, have retained their resistance to arsenic. Evidence is presented which suggests that these ticks can be controlled by DDT. Toxaphene and high concentrations of gamma BHC also exercise some degree of control in the field. The experiments were carried out over two consecutive years.

Method.

In the laboratory experiments various insecticidal preparations were analysed chemically to check dilution rates, and were examined biologically. Total hydrolysable chlorine was determined in the chemical analyses and, in the case of BHC, the gamma isomer content was calculated from these determinations on the basis that the crude product contained 10 per cent. Determinations of p,p′ DDT were made in a similar manner. No chemical analyses were undertaken for toxaphene or chlordane. Biological examinations were an essential part of the investigation and the *in vitro* technique followed was that described by Whitnall and Bradford (1947), a technique which has been found thoroughly reliable. Tick material was obtained from farms where BHC dips failed to control blue ticks and, from other localities such as " Henley ", on the Fish River, where ticks were known to be BHC-sensitive. The insecticidal susceptibility of ticks from different localities was thus compared.

The field experiments were carried out on farms where the blue tick was not controlled by regular dippings in BHC. Cattle were dipped or sprayed at weekly intervals, and samples of dip-wash were taken for chemical and biological assay. Samples of spray-wash were also taken but, as freshly mixed sprays were known to maintain their biological activity, they were not examined regularly as were the dip-wash samples which might deteriorate (Whitnall & others, 1948). The female blue ticks for these examinations came from " Henley ". The evaluation of the field results was based on examinations of scrapings taken from the necks of treated and untreated animals. Details of the method were devised by Thorburn, and were an improvement on those used by Whitnall and Bradford (1949). They consisted of the following routine procedure :—

The experimental groups consisted of three animals all of which were noticeably infested with blue ticks (Pl. IV, fig. 1). The animals were distinctively marked and, as all grazed in the same camps, they were exposed to the same possibilities of infestation by ticks. Just before each weekly treatment scrapings were taken from the necks of two animals in each group. They were taken with a curved metal grape fruit knife in rotation from one of four zones of the neck, an upper and a lower on the left and right sides. In this way each zone was scraped every fourth week, so that sufficient time was allowed between scrapings for the normal development of the one host blue tick on any zone. Weekly scrapings from both animals in a group were collected in a specially constructed metal funnel, corked at the narrow end (Pl. IV, fig. 2). They always contained much hair and scurf in addition to the various stages of ticks and other ectoparasites and, were washed out of the funnel into an Erlenmeyer flask with 50 per cent. alcohol. This killed the ticks and preserved them for later examination. When preparing the material for examination, 100 ccs. of 10 per cent. caustic potash were added to the Erlenmeyer flask and the whole heated to boiling point. This dissolved the keratin and so destroyed the hair and scurf, while the chitinous exoskeletons of the ticks and other parasites remained undamaged. When cool, the contents of the flask were distributed over a piece of organdie marked in $\frac{1}{2}$-in. squares, and stretched tightly over a 5×8-in. wooden frame. The fine mesh of the organdie retained all stages of ticks, and allowed the dissolved keratin to pass. The surface of the organdie was washed gently with water and the ticks distributed more evenly. The frame with its contents was then placed over a white enamel basin for examination, which was best completed while the organdie and contents were moist. The examinations were carried out under a binocular microscope (12×), and all stages of the blue tick were counted. Scrapings were classified into larvae, nymphs and adult ticks, the latter group being further divided into males and females. Engorgement of larvae was also recorded. Other tick species and ectoparasites were discarded. The results of these counts are presented in a series of histograms, figs. 1 to 3.

Laboratory Investigations.

Experiments with ticks in the Eastern Cape Province have been carried on since 1940. From 1945, when the *in vitro* technique was standardised, to February 1948, 215 separate laboratory experiments were conducted involving the treatment of 50,641 adult female blue ticks. Fresh dilutions of standard BHC preparations containing 50 p.p.m. (0·005 per cent.) gamma isomer always gave results approximating 100 per cent. control. Even 25 p.p.m. gave striking results. It was against this background of data that the following experiments were conducted.

East London Ticks.

In March 1948, at the farm " Burnside " in the East London district, cattle receiving weekly dippings became heavily infested with blue ticks. The wash, which was made up from a BHC dispersible paste and arsenite of soda, contained over 50 p.p.m. gamma isomer and 0·12 per cent. As_2O_3. Simultaneously at the East London farm " Mistley ", blue ticks developed on cattle in spite of weekly dippings in a dispersible paste wash containing 89 p.p.m. gamma isomer. Adult female ticks from " Burnside " and " Mistley " were tested *in vitro* in their respective samples of dip-wash and fresh dilutions of paste, while blue ticks from " Kenton-on-Sea ", in the Alexandra district, where they are known to be BHC-sensitive, were given the same *in vitro* treatments. The results are presented in Table I.

TABLE I.

Treatment of BHC-resistant (" Burnside " and " Mistley ") and BHC-sensitive (" Kenton-on-Sea ") ticks with field samples of freshly prepared BHC formulations.

Treatment	gamma isomer p.p.m.	% As_2O_3	" Burnside " ticks				" Mistley " ticks				" Kenton-on-Sea " ticks			
			No. of ticks	% ♀♀ laid	% batches hatched	% control	No. of ticks	% ♀♀ laid	% batches hatched	% control	No. of ticks	% ♀♀ laid	% batches hatched	% control
Water	—	—	20	100	90	10	20	100	100	0	20	100	100	0
" Burnside " dip-wash sample 4.iii.1948 ...	59	·12	50	96	98	6	—	—	—	—	50	66	94	38
" Burnside " dip-wash sample 10.iii.1948 ...	54	·12	50	100	92	8	—	—	—	—	50	60	97	42
" Mistley " dip-wash sample 10.iii.1948 ...	89	—	—	—	—	—	20	95	90	15	20	15	0	100
Freshly diluted BHC paste	56	—	50	98	98	4	20	85	88	25	50	8	0	100
Freshly diluted BHC paste	28	—	50	100	96	4	20	100	95	5	50	10	80	92

Twenty-four hours after treatment it was apparent that strains of blue ticks reacted differently to the same concentrations of gamma isomer. " Kenton-on-Sea " ticks were characteristically flattened, grooved and curved while " Burnside " and " Mistley " ticks were unaffected. " Kenton-on-Sea " ticks responded readily to treatment, as fresh dilutions of the paste at 56 and 28 p.p.m. gamma isomer gave 100 per cent. and 92 per cent. control, results which were in line with those generally obtained with blue ticks. " Burnside " and " Mistley " ticks responded very differently, both concentrations having little effect upon them.

Polluted dip-wash samples from " Burnside " which contained BHC and arsenic, had little effect upon " Burnside " ticks, but some effect upon those from " Kenton-on-Sea ". Likewise the " Mistley " sample had little effect on the " Mistley " ticks, but gave 100 per cent. control of " Kenton-on-Sea " ticks. The positive reactions of " Kenton-on-Sea " ticks to 28 and 56 p.p.m. gamma isomer in fresh dilutions of paste, compared with their poor reactions in the " Burnside " samples with 54 and 59 p.p.m. gamma isomer, suggested that the biological activity of the latter had been impaired. This aspect of the problem has been studied (Whitnall & others, 1948), but falls outside the scope of the present paper.

In further *in vitro* experiments with BHC-resistant ticks, only freshly diluted preparations were used. The formulations tested consisted of a dispersible paste ; an oil in water emulsion, the oil phase being a solution of crude BHC in a mixture of coal tar and mineral oils ; and a solution of the pure gamma isomer in alcohol. Dilutions of these preparations were tested against blue ticks from East London, and also from Bathurst and Albany districts. The results of some tests are given in Tables II and III.

TABLE II.

Treatment of BHC-resistant and BHC-sensitive ticks with freshly prepared BHC formulations.

Treatment	gamma isomer p.p.m.	" Gulu " ticks			" Barville Park " ticks		
		% ♀♀ laid	% batches hatched	% control	% ♀♀ laid	% batches hatched	% control
Water	—	100	100	0	100	96	4
Freshly diluted BHC paste	48	92	96	12	16	25	96
Freshly diluted BHC paste	104	76	95	28	8	0	100
Freshly diluted BHC paste	157	68	94	36	12	0	100
Freshly diluted BHC emulsion	32	100	96	4	16	0	100
Freshly diluted BHC emulsion	57	88	86	24	4	0	100
Freshly diluted BHC emulsion	179	72	94	32	4	0	100

Twenty-five ticks in each treatment.

TABLE III.

Treatment of BHC-resistant and BHC-sensitive ticks with freshly prepared BHC formulations.

Treatment	gamma isomer p.p.m.	" Mistley " ticks			" Henley " ticks		
		% ♀♀ laid	% batches hatched	% control	% ♀♀ laid	% batches hatched	% control
Water	—	100	95	5	100	90	10
8·7 per cent. alcohol ...	—	100	95	5	95	95	10
Suspension of pure gamma isomer in 4·4 per cent. alcohol	41	88	83	27	8	0	100
Suspension of pure gamma isomer in 8·7 per cent. alcohol	82	65	77	50	3	0	100
Freshly diluted BHC emulsion	32	100	100	0	28	64	82
Freshly diluted BHC emulsion	57	95	97	10	5	0	100

Twenty ticks in water and alcohol, 40 ticks in other treatments.

"Gulu" ticks came from the third farm near East London where weekly dippings in BHC failed to control them. Table II shows that neither the paste nor the emulsion preparations were effective against these ticks and even concentrations of 157 and 179 p.p.m. gamma isomer failed to give 100 per cent. control. Ticks from "Barville Park" in the Bathurst district reacted normally. Table III compares "Mistley" ticks with those from "Henley" in the Albany district. The former showed marked resistance to all BHC preparations, while the latter responded as expected.

Bathurst Ticks.

An experiment with bont ticks was started at "Tharfield" in the Bathurst district in October 1948. A BHC oil-emulsion dip was used, first at 50 and later at 100 p.p.m. gamma isomer. The wash was kept biologically active at these concentrations by weekly additions of fresh dip. The bont tick was controlled (Whitnall & others, 1951), but heavy infestations of blue tick developed on cattle which grazed in certain camps, in spite of regular weekly dippings. This was first noted in December 1948, when adult female blue ticks became readily available and *in vitro* tests were carried out. The results of one such test are given in Table IV, which clearly indicates the resistance of "Tharfield" ticks to BHC compared with the sensitive "Henley" ticks.

TABLE IV.

Treatment of BHC-resistant ticks from Bathurst district and BHC-sensitive ticks from Albany district with different formulations.

Treatment	Concentration p.p.m.	"Tharfield" ticks			"Henley" ticks		
		% ♀♀ laid	% batches hatched	% control	% ♀♀ laid	% batches hatched	% control
Water	—	100	100	0	95	100	5
BHC paste ...	95 gamma isomer	100	95	5	5	0	100
BHC paste + DDT dispersible powder	50 gamma isomer + 1,000 p,p′DDT	50	30	85	0	0	100
BHC emulsion ...	100 gamma isomer	100	100	0	5	0	100
BHC emulsion ...	500 gamma isomer	80	100	20	5	0	100

Twenty ticks in each treatment.

In March 1949 BHC dips were found to be ineffective against blue ticks on other farms in the Bathurst district. Ticks from "Elmhirst", on the west bank of the Kowie River, were treated *in vitro* in freshly diluted paste containing 50 and 100 p.p.m. gamma isomer. Only 15 per cent. control was obtained in both dilutions, while the treatments gave 100 per cent. control of "Henley" ticks.

Tests with other Insecticides.

A number of laboratory experiments using BHC-resistant and sensitive ticks were carried out with other insecticides including DDT, toxaphene and chlordane. At the same time high concentrations of gamma BHC, and supplies from different sources, were tested. The results of some experiments are given in Table V.

TABLE V.

Tests with various insecticides against BHC-resistant (" Burnside ") and BHC-sensitive (" Henley ") ticks.

Treatment	Concentration p.p.m.	" Burnside " ticks			" Henley " ticks		
		% ♀♀ laid	% batches hatched	% control	% ♀♀ laid	% batches hatched	% control
Water	—	95	100	5	95	100	5
0·16 per cent. As_2O_3	—	90	95	15	90	61	45
DDT emulsion ...	2,000 p,p'DDT	50	100	50	25	60	85
DDT wettable powder	2,500 p,p'DDT	40	0	100	—	—	—
DDT wettable powder	5,000 p,p'DDT	45	11	95	—	—	—
Toxaphene emulsion	2,000 toxaphene	100	95	5	10	0	100
Toxaphene emulsion	4,000 toxaphene	95	95	10	0	0	100
Toxaphene emulsion	8,000 toxaphene	100	100	0	0	0	100
Chlordane emulsion	500 chlordane	95	95	10	0	0	100
BHC paste ...	103 gamma isomer	95	90	15	0	0	100
BHC paste ...	1,000 gamma isomer	40	13	95	0	0	100
BHC dispersible powder	100 gamma isomer	95	95	10	10	0	100
BHC dispersible powder	500 gamma isomer	55	64	65	0	0	100
BHC emulsion (*a*)	100 gamma isomer	95	95	10	5	0	100
BHC emulsion (*b*)	97 gamma isomer	100	100	0	5	0	100
BHC emulsion (*b*)	489 gamma isomer	95	68	35	5	0	100

Twenty ticks in each treatment.

Ticks from the two localities, " Burnside " and " Henley ", reacted very differently except to treatments in arsenic and DDT. Both appear to be arsenic-resistant. DDT, although giving a fairly high degree of control, is not entirely satisfactory, as there has been a high percentage lay in both cases and some ova were viable.

Toxaphene, chlordane and BHC were effective against " Henley " ticks, as all gave 100 per cent. control. " Burnside " ticks exhibited a marked degree of resistance to the three insecticides. As the BHC in the paste and dispersible powder, and in emulsions (*a*) and (*b*) came from different sources, there is nothing in the claim that method of manufacture may be responsible for the ineffectiveness of BHC.

Field Investigations.

First Experiment at "Burnside" in East London District.

Field experiments, that were carried out at the same time, confirm the laboratory tests. At "Burnside" the dipping tank was filled with a BHC emulsion dip at the rate of 1 gallon of 25 per cent. BHC emulsion to 250 gallons water (100 p.p.m. gamma isomer), and 1 gallon of emulsion concentrate was added for every 250 cattle dipped to offset an anticipated drop in concentration. The chemical and biological results, the latter obtained with "Henley" blue ticks, presented in Table VI, show that it was successful.

TABLE VI.

Chemical and biological data relating to dip samples taken from "*Burnside*".
Emulsion dip.

Sample No. and date	No. cattle dipped	Replenishments		Chemical data	Biological data			
		Water gals.	Dip gals.	gamma isomer p.p.m.	% ♀♀ laid	% batches hatched	% control	Water % control
1. 17.xi.1948 ...	184	3,000*	12*	88	5	0	100	0
2. 24.xi.1948 ...	189	—	2½	98	0	0	100	0
3. 1.xii.1948 ...	181	100	¾	92	25	20	95	0
4. 8.xii.1948 ...	188	—	1	96	0	0	100	15
5. 15.xii.1948 ...	188	—	½	95	35	57	80	15
6. 22.xii.1948 ...	180	—	1	76	10	0	100	10
7. 29.xii.1948 ...	186	450	2½	80	5	100	95	10
8. 5.i.1949 ...	180	—	1	—	10	50	95	10
9. 12.i.1949 ...	183	200	3½	97	15	33	95	10
10. 19.i.1949 ...	183	—	1	98	10	50	95	10
11. 26.i.1949 ...	183	—	2	119	0	0	100	0
12. 2.ii.1949 ...	190	650	3⅝	115	10	0	100	10

Twenty ticks in each sample and in water.
*These figures represent the amounts of water and dip respectively put into the tank originally.

The experiment continued for 12 weeks from 17th November 1948 to 2nd February 1949 and included application of washes by spraying as well as by dipping. Groups of three animals were given the following treatments each week : (1) Untreated. (2) Dipped in emulsion wash, 100 p.p.m. gamma isomer. (3) Sprayed with emulsion wash, 100 p.p.m. gamma isomer. (4) Sprayed with emulsion wash, 500 p.p.m. gamma isomer and (5) Sprayed with dispersible paste wash, 100 p.p.m. gamma isomer. Prior to each treatment, scrapings were taken from the necks of two animals in each group. The results are presented in fig. 1.

Larvae, nymphs and adults were found on all five groups, indicating that larvae of the one host blue tick had survived the weekly treatments. During the last 2 weeks of December, no nymphs and only a few adults appeared on the animals sprayed with 500 p.p.m. gamma isomer, but with the general increase in tick life on the pastures, which was indicated by the large numbers of larvae scraped from all animals after December, even this concentration failed to prevent development of nymphs and adults.

Second Experiment at "Burnside".

The second experiment at "Burnside" began on 16th February 1949, and continued for 12 weeks. The tank was filled with a dispersible powder dip at 3 lb. per 100 gals. water which gave a concentration of more than 100 p.p.m. gamma isomer and the tank was replenished from time to time by the addition of water and dip to offset any fall in concentration. This dip contained BHC of a different origin from that in the emulsion used in the first experiment. From Table VII it will be seen that samples of wash remained biologically active.

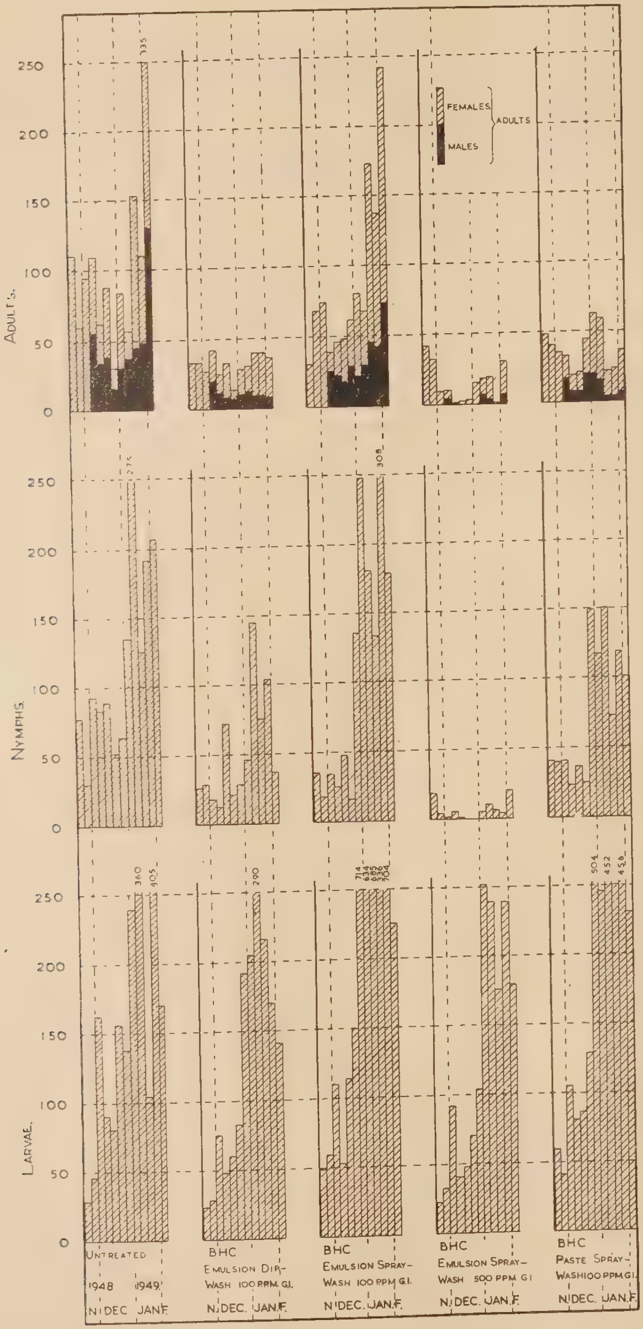

Fig. 1.—Weekly counts of larval, nymphal and adult blue ticks scraped from the necks of two animals in groups which received different weekly BHC treatments. All animals grazed in the same camp at " Burnside ".

TABLE VII.

Chemical and biological data relating to dip samples taken from " Burnside ".
Dispersible powder dip.

Sample No. and date	No. cattle dipped	Replenishments		Chemical data	Biological data			
		Water gals.	Dip lb.	Gamma isomer p.p.m.	% ♀♀ laid	% batches hatched	% control	Water % control
1. 16.ii.1949 ...	170	3,000*	90*	122	0	0	100	5
2. 23.ii.1949 ...	175	150	6	126	0	0	100	5
3. 2.iii.1949 ...	170	300	12	107	0	0	100	5
4. 9.iii.1949 ...	170	—	—	107	10	100	90	0
5. 16.iii.1949 ...	170	500	20	113	10	50	95	0
6. 23.iii.1949 ...	170	—	—	119	0	0	100	0
7. 30.iii.1949 ...	148	—	—	124	5	0	100	0
8. 6.iv.1949 ...	150	—	—	135	10	0	100	0
9. 13.iv.1949 ...	150	750	22½	141	5	0	100	5
10. 20.iv.1949 ...	150	250	5	140	0	0	100	5
11. 27.iv.1949 ...	150	350	7	136	10	0	100	0
12. 4.v.1949 ...	167	—	—	136	10	0	100	0

Twenty ticks in each sample and in water.
*These figures represent the amounts of water and dip respectively put into the tank originally.

Weekly dippings failed to prevent the development of " Burnside " blue ticks on the cattle. Scrapings from the dipped animals contained larvae, nymphs, males and females in approximately the same numbers as appeared on untreated animals (fig. 2).

Other groups of three animals were treated weekly as follows :—Sprayed with BHC dispersible powder wash, 100 and 1,000 p.p.m. gamma isomer ; sprayed with 5,000 and 2,500 p.p.m. toxaphene emulsion ; sprayed with dispersible powder spray, 5,000 and 2,500 p.p.m. p,p′DDT ; sprayed with BHC dispersible paste, 1,000 p.p.m. gamma isomer ; sprayed with 0·16 per cent. $As_2 O_3$; and sprayed with 2,500 p.p.m. chlordane emulsion. Counts of scrapings from these groups are also presented in fig. 2.

The dispersible powder spray when used at 100 p.p.m. gamma isomer was as ineffective as the dip. Both powder and paste when used at 1,000 p.p.m. gamma isomer largely prevented the development of larvae, and gave results which were comparable with those obtained with 50 p.p.m. in 1946–47 when BHC was first used.

Toxaphene prevented the development of larvae, and thus controlled the ticks. At 5,000 p.p.m. no males or females were found on the animals during the last six weeks of the experiment.

The most striking results were obtained with DDT. Weekly sprayings with 5,000 p.p.m. p,p′DDT kept the animals free from nymphs, males and females for eight weeks.

Weekly sprayings with 0·16 per cent. $As_2 O_3$ failed to control the blue ticks, and thus confirmed the laboratory findings that the ticks were still arsenic-resistant.

Chlordane was tested for a short period. It gave disappointing results at the concentration used.

Experiment at " Tharfield " in Bathurst District.

An experiment in the Bathurst district was carried out at " Tharfield ". It began on 22nd February 1949, and continued for nine weeks. The experimental groups of cattle were treated as follows :—(1) Untreated, (2) dipped in BHC emulsion dip-wash, 100 p.p.m. gamma isomer, (3) sprayed with 0·16 per cent. $As_2 O_3$ solution (4) sprayed

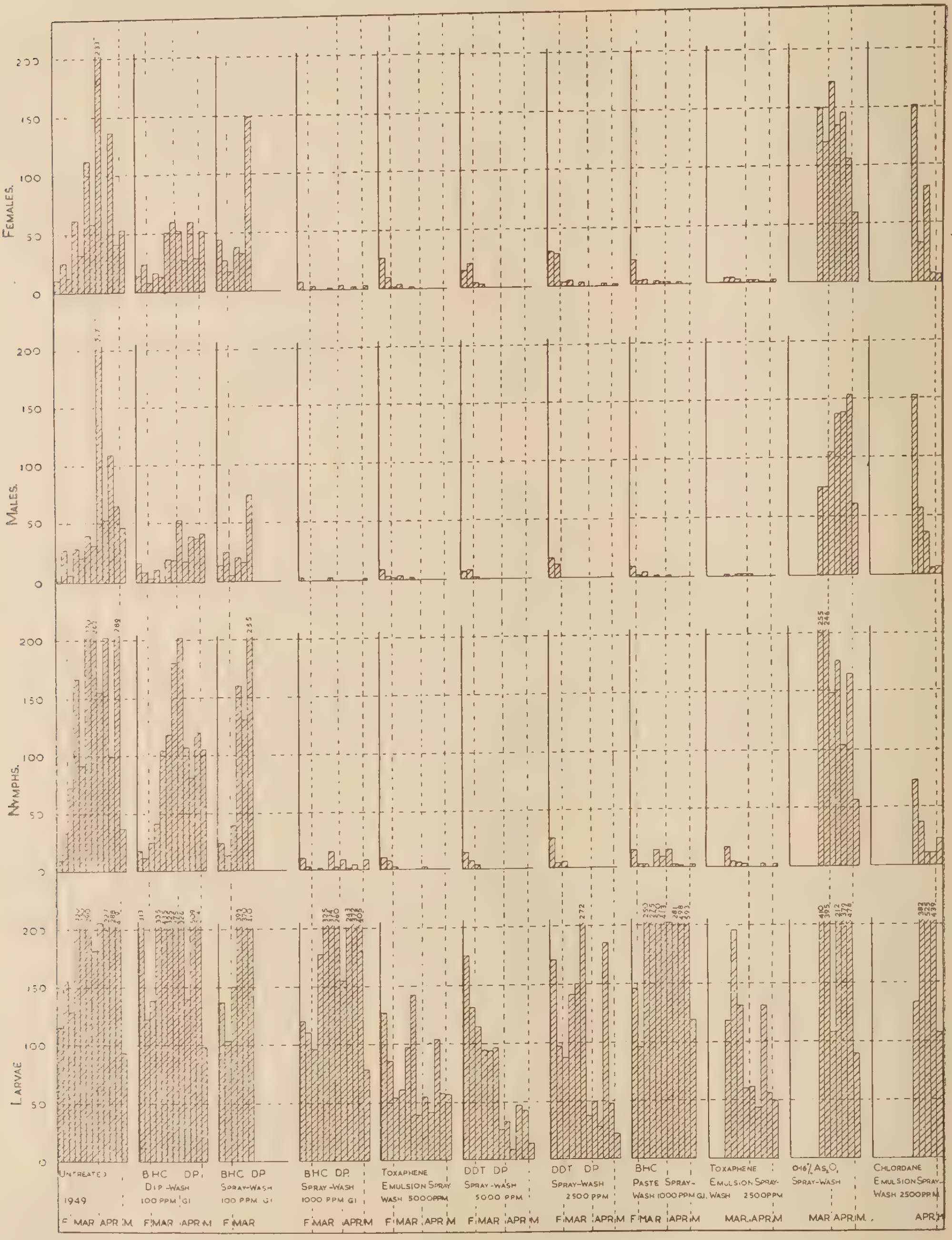

Fig. 2.—Weekly counts of larval, nymphal, male and female blue ticks scraped from the necks of two animals in groups which received different weekly treatment. All animals grazed in the same camp at " Burnside ".

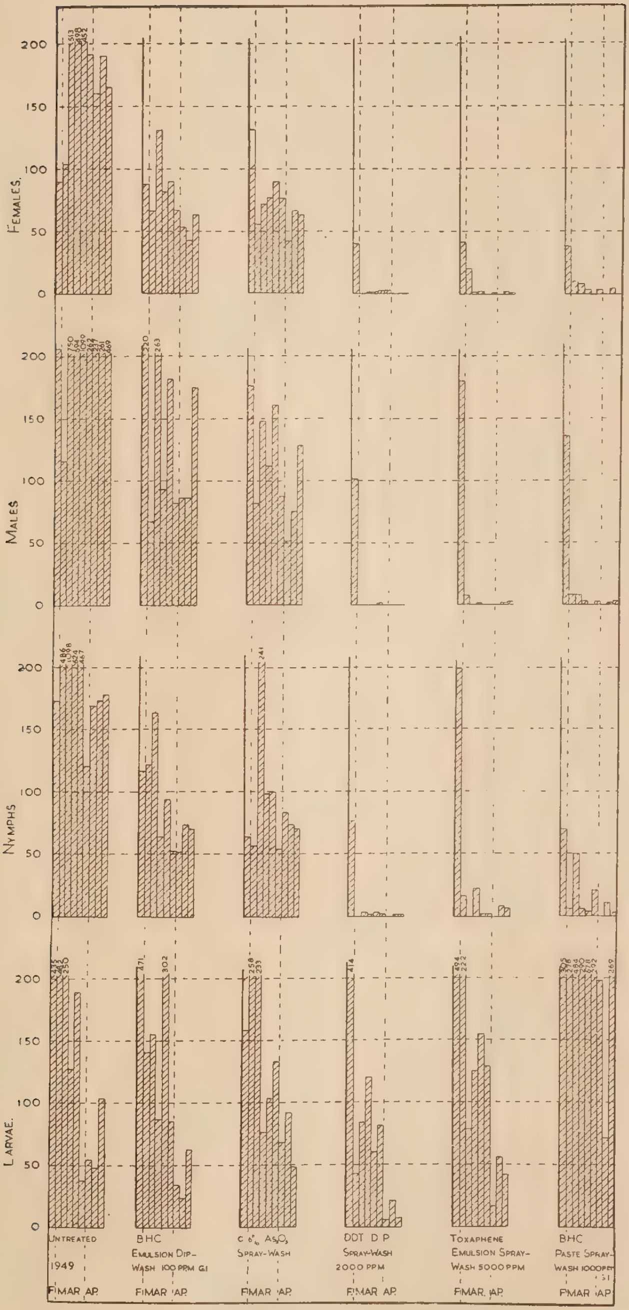

Fig. 3.—Weekly counts of larval, nymphal, male and female blue ticks scraped from the necks of two animals in groups which received different weekly treatments. All animals grazed in the same camp at " Tharfield ".

with dispersible powder spray-wash, 2,000 p.p.m. p,p′DDT, (5) sprayed with emulsion spray-wash, 5,000 p.p.m. toxaphene, and (6) sprayed with BHC dispersible paste spray-wash, 1,000 p.p.m. gamma isomer.

The emulsion dip used in this experiment was the same type as that in the first experiment at " Burnside " and was used in the same manner. During the nine weeks of the experiment, the estimated gamma isomer content of the wash ranged from 109 to 114 p.p.m. The wash remained biologically active, the control of " Henley " ticks ranging from 85 per cent. to 100 per cent. in *in vitro* tests. Weekly dippings in this wash controlled the bont tick, but blue ticks developed on the cattle, as the analyses of scrapings presented in fig. 3 show.

Weekly sprayings with 0·16 per cent. $As_2 O_3$ did not control " Tharfield " blue ticks, as large numbers of larvae developed into adults on animals so treated.

DDT, toxaphene and high concentrations of gamma BHC prevented many larvae from developing further and gave results comparable with those of the second " Burnside " experiment.

Discussion.

The experiments prove that a BHC-resistant strain of the blue tick, *B. decoloratus*, has developed. It appeared early in 1948 in the East London district, where the arsenic-resistant strain first appeared. The distribution of the BHC-resistant tick was at first limited to " Mistley ", " Burnside " and " Gulu " near East London but late in 1948 it appeared at " Tharfield ", and early in 1949 it was recorded from " Elmhirst ", in the Bathurst district. The arsenic-resistant tick appeared ten years previously in the East London district and shortly afterwards became numerous on coastal farms at Bathurst. It is remarkable that these two strains of ticks should appear in the same localities.

It would appear that once a resistance has developed that it may possibly become an inherent character, for farms which had arsenic-resistant blue ticks in 1939 still had them ten years later, in spite of a long period of dipping in non-arsenical washes. Arsenic-resistance appears to be associated with BHC-resistance, for no instance has been found where ticks are resistant to BHC without being resistant to arsenic. Arsenic-resistance developed many years after the first use of arsenic but the development of BHC-resistance took place in a remarkably short time, only 18 months from the first use of the dips in the field. It may be of interest to record that the areas where the ticks resistant to arsenic and BHC and those non-resistant are found, differ climatically. The resistant ticks have appeared first in the coastal belt, which has a higher rainfall, and is more humid than the higher and drier farm " Henley ".

The development of resistance is not fully understood and might be explained in a number of ways. It appears to be associated with an internal change of the tick rather than a mechanical resistance, for the arsenic-resistant tick was at first readily killed by BHC. It is possible that there has been unintentional artificial selection within the tick population of those mutants which happen to be resistant to the poison. The continued use of the poison would then result in the establishment of a strong stock of ticks, as was the case with DDT-resistant house-flies in Florida, U.S.A. (Lindquist & Wilson, 1948 ; Wilson & Gahan, 1948). In the case of BHC and the tick, this was not due to the fact that the chemical was first used at too low a concentration, although any such tendency would be accentuated by the fact that BHC loses its biological activity in foul dipping tanks (Whitnall & others, 1948). The appearance of the BHC-resistant tick seems too rapid for such an explanation. It is possible that once the tick is resistant to arsenic, the organism is in a state of " flux " and any new unusual external stimulus induces an internal change, possibly some chromosome change, which, when once it has taken place remains and becomes an inherited character. This character might be resistance to a chemical used, and would support the view that a mass transformation is taking place. This theory is largely supported by the rapid appearance and spread of the BHC-resistant tick. It is also possible, bearing in mind the reproductive powers of the blue tick, that the resistant strain has developed from a single mutant. This hypothesis is unlikely for the rapid spread of the resistance is difficult to explain on this basis. Early in this study an attempt was made to learn something about the genetics of ticks, but it was found impossible with the facilities available.

Whatever may be the explanation for this bio-chemical development it is of the utmost importance both scientifically and economically. A closer study of the physiology of insects and other Arthropod pests in relation to the action of insecticides is clearly indicated. The *in vitro* experiments suggested that the action of DDT on BHC-resistant and BHC-sensitive ticks is similar. The chlorinated cyclic hydrocarbons, toxaphene and chlordane were ineffective against BHC-resistant ticks, but killed BHC-sensitive ticks. These findings are comparable with those of Keiding and van Deurs (1949) who showed that DDT-resistant flies were also resistant to other compounds with a DDT-like structure, but reacted uniformly with other flies towards the cyclic hydrocarbons.

The laboratory experiments with adult female ticks suggested that DDT would give only moderate field results. This was in line with results by Arnold (1949), who reported variable and on the whole less satisfactory results than those obtained in field control with DDT when used in *in vitro* experiments against adult female *B. annulatus* var. *microplus* (Can.). The striking results of field experiments with DDT suggest an action on some other stage of the tick. They could be explained by the excitant and repellent action of DDT reported by Kennedy (1947) and Muirhead-Thomson (1949) in their work with mosquitos. The small numbers of larvae scraped from DDT-treated animals compared with those from other groups, particularly those treated with BHC, might be taken to indicate a repellent action. With BHC, Muirhead-Thomson found no indication of irritation similar to that which drove mosquitos out of DDT-treated houses. Alternatively, the persistent action of DDT might kill many larval ticks attempting to attach. These would fall off and not be recorded in the scrapings. Similar explanations are offered for the contradictory *in vitro* and field results with toxaphene against BHC-resistant ticks.

At present weekly dippings in DDT washes containing at least 0·15 per cent. p,p′ DDT effect control of the BHC-resistant tick by preventing larval development. It is not known how long this will continue, for it is possible that this tick, which has become resistant to arsenic and BHC, may in turn become resistant to DDT.

Summary.

An arsenic-resistant tick was first noticed in the East London district of South Africa in 1938–39. It was a strain of the one host blue tick, *B. decoloratus*. BHC was very toxic to the tick, as 50 p.p.m. of the gamma isomer killed adult females in *in vitro* experiments. Field results in 1946–47 were equally convincing. Weekly dippings in BHC washes containing 50 p.p.m. gamma isomer brought the arsenic-resistant tick under control.

In March 1948, BHC was found to be ineffective against blue ticks at " Burnside ", " Mistley " and " Gulu ", farms in the East London district. Later, ticks at " Tharfield " and " Elmhirst " in the Bathurst area survived regular weekly dippings in BHC preparations. *In vitro* experiments showed that adult female blue ticks taken from these localities could withstand high concentrations of gamma BHC, while females of the same species from other areas were readily killed. Not even 1,000 p.p.m. would give 100 per cent. control of ticks from resistant areas, and different sources of gamma BHC were equally ineffective. Laboratory experiments further indicated that the ticks were still arsenic-resistant. Indeed arsenic resistance appears to be associated with BHC resistance, as no BHC-resistant tick has been found that is not arsenic-resistant. The chlorinated cyclic hydrocarbons toxaphene and

chlordane were ineffective against BHC-resistant ticks, but controlled BHC-sensitive ticks in the laboratory. DDT gave moderate *in vitro* results against both resistant and sensitive ticks.

In field experiments weekly treatments in 0·16 per cent. As_2O_3 failed to control blue ticks on cattle at "Burnside" and "Tharfield". The ticks also developed normally at both farms when cattle were treated weekly with 100 p.p.m. gamma BHC. Even 500 p.p.m. was unsatisfactory at "Burnside". In 1949, 1,000 p.p.m. gamma isomer was necessary to give results comparable with those obtained with 50 p.p.m. in 1947.

DDT and toxaphene gave good results in the field. These are not fully understood for *in vitro* tests suggested that only moderate and poor results respectively could be expected against BHC-resistant ticks. The residual or persistent toxic action of these insecticides, by killing many larvae which are attempting to attach themselves, might account for these favourable results. Alternatively the good results might be due to excitant and repellent action. This would account for the small numbers of larvae, and consequent absence of nymphs and adults, on animals treated with DDT and toxaphene.

The BHC-resistant strain of *B. decoloratus* appeared in the same localities as those in which the arsenic-resistant strain first appeared some 10 years previously. Furthermore it is evident that in these two areas, East London and Bathurst districts, the resistance is spreading rapidly. The development took place only 18 months after the first use of BHC dips in the field.

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Mr. W. T. Willows of "Burnside" and Mr. V. Webb of "Tharfield" placed dipping tanks, cattle and labour at our disposal, and cheerfully assisted with the field work. Mr. P. White of "Henley" left his herds of cattle undipped to breed ticks for our *in vitro* experiments.

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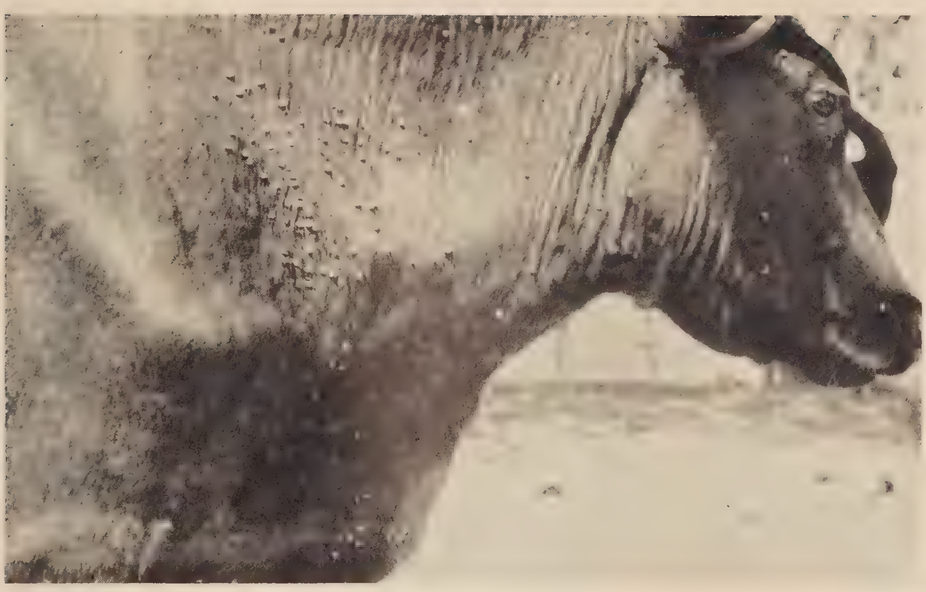

FIG. 1. Blue ticks on the neck of a cow at "Tharfield" in the Bathurst area. These ticks developed in spite of the fact that the B.H.C. dip controlled the Bont Tick.

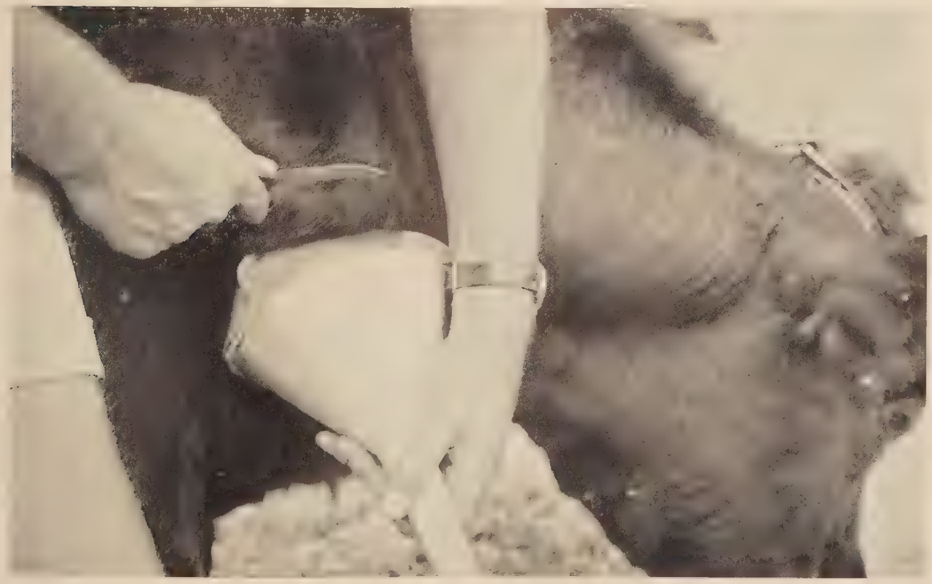

FIG. 2. Larvae, nymphs and adults of the one host blue tick, if present, were readily scraped from the host and collected as shown.

STUDIES OF TOXICITY OF 3 : 5 DINITRO-ORTHO-CRESOL AND ITS SODIUM SALT TO THE HONEY BEE.

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The chemicals 3 : 5-dinitro-ortho-cresol (numbered with CH_3 as 1) and its sodium salt—hereafter referred to as DNOC and sodium DNOC respectively—are commonly used as weed killers. They are used for the control of charlock (*Sinapis arvensis* L.) which might be in flower when sprayed, and they are being developed as blossom-thinning sprays.

Ginsburg (1929) reported that DNOC was toxic to the honey bee and he stated that bees fed on a 0·01 per cent. emulsion in honey were dead in five hours. Rodríguez Icart (1947) discussed the losses of honey bees in Uruguay due to the use of DNOC to kill red locusts and he reported that bees dusted with the chemical died in five to seven minutes ; a film of this material exposed for two days killed bees in 10 to 12 minutes, and a film exposed for three days killed in 18 minutes. He considered that the contaminated bees would not reach the hive owing to the speed of toxic action. Hives near areas where dusting had taken place showed little loss. Schneider (1945) reported that winter sprays containing DNOC could poison bees in search of water in late February or early March. Goble and Patton (1946) found that salts of DNOC are highly toxic to the honey bee and that they do not decompose but remain potentially toxic for some time after application. Eide (1947) considered dinitro compounds including DNOC to be highly toxic to the honey bee. In the United States of America it is considered that the greatest threat to the honey bee occurs when dinitro compounds are used for thinning apple blossom. Some losses have been reported in Great Britain and France due to the use of DNOC to control charlock.

Laboratory Experiments.

Methods.

Preliminary experiments with different types of cages showed that adequate ventilation is necessary to prevent a rise of humidity within the cage.

The design finally adopted for use after spray treatment consisted of a 3 × 1-in. tube of perforated zinc corked at one end with a glass U tube inserted in the wall into which sucrose solution was introduced. Five of these tubes were soldered on to a base plate of zinc. This type of cage was also found to be particularly satisfactory for the stomach poison tests when the bees were caged individually. Normally five bees were put into each cage.

After treatment the bees were caged and placed in a constant temperature cabinet at 30°C. with a relative humidity of approximately 50 per cent. The mortality was measured at intervals up to 24 hours, this time being selected for the following reasons :—

(1) The caging of bees inhibits defaecation and some poisons may be retained in the bee which would be voided under natural conditions.

(2) DNOC is known to be a rapidly acting poison.

(3) A 100 per cent. survival of the control bees is easily achieved for 24 hours.

Toxicity of aqueous sprays of DNOC and sodium DNOC.

A modification of the laboratory spraying apparatus described by Potter (1941) was used for these tests. Thirty bees were used at each concentration and before spraying they were anaesthetised with carbon dioxide and placed on a petri dish lined with filter paper.

A stable emulsion of DNOC was prepared by dissolving 1·0 gm. of the pure acid in 5 ml. of benzene and pouring this into 200 ml. of distilled water containing 0·05 per cent. cyclohexylamine dodecyl sulphate. The emulsion was vigorously agitated before use. A solution of sodium DNOC was prepared by neutralising 1 gm. of the pure acid with a calculated amount of N.NaOH.

Pradhan (1949) showed that the toxicity of DNOC to adult *Tribolium castaneum* (Hbst.) was dependent on the humidity during treatment and in order to consider the effect of humidity, two groups of bees were sprayed at each concentration one being kept at a relative humidity of 45–50 per cent. and the other at 85–90 per cent.

TABLE I.

Comparison of acid and salt as contact poisons sprayed at the same equivalent concentrations of the acid, under differing humidities.

Deposit in mg. per sq. cm.	Percentage kill with acid		Percentage kill with salt	
	R.H. 45–50%	R.H. 85–90%	R.H. 45–50%	R.H. 85–90%
0·048 ...	100	100	69	100
0·024 ...	100	100	20	100
0·0097 ...	40	70	3	35
0·0048 ...	13	36	6	10
0·00097 ...	6	10	3	0
Controls ...	6	0	3	3

The results shown in Table I indicate that both the salt and acid are toxic to the honey bee in aqueous medium as a contact poison and that the humidity of the environment exerted an effect on toxicity which was most marked with the sodium salt. At the lower range of humidity the sodium salt was much less toxic than the acid but at high humidities both acid and salt were very similar in action. The acid appeared to be slightly less toxic when the bees were kept at the lower humidity.

In the above experiment most of the deaths occurred within two hours of treatment which indicated that the poisons were fairly rapid in action.

An attempt was made to investigate in greater detail the effect of differing environmental humidities on the toxicity of the sodium salt but the results obtained fluctuated very erratically, *e.g.*, a 0·5 per cent. solution sprayed on to two lots of 20 bees kept at 50 per cent. R.H. produced kills after 24 hours, of 19 in the one case and only two in the other. It appeared that the time the spray took to dry on the bees affected the toxicity and this was related to the time taken to recover from the anaesthetic. The spray dried quickly when the bees became active in the cages.

Attempts were also made to keep bees in small constant humidity chambers such as those used by Pradhan (1949) but owing to the high metabolic activity of the honey bee they were not successful.

Toxicity of films of DNOC and sodium DNOC.

In order to test the effect of residual insecticidal deposits on honey bees, Filmer & Smith (1944) used wire screen cages which they put over glass plates, on which deposits of the insecticides had been placed. This did not allow all the bees to be

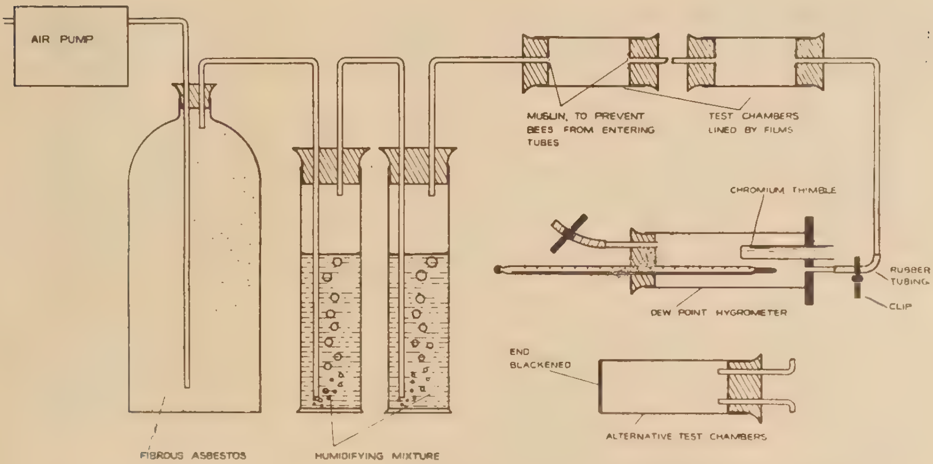


Fig. 1.—Apparatus for exposure of honey bees to insecticidal films under conditions of controlled humidity.

kept continuously in contact with the films and later they attempted to overcome this difficulty by placing the films on the inside of glass tubes.

For the present experiments a technique was sought whereby the bees might be exposed continuously to the films and in which it would be possible to vary temperature and humidity. Initial attempts did not allow sufficient ventilation of the air space around the films and moisture tended to condense on the various surfaces due to the high metabolic activity of the honey bee. Difficulties were also encountered in keeping the bees on the surface of the films.

The apparatus as shown in fig. 1 was finally adopted. The test chambers used were glass tubes measuring 10×3·5 cms., fitted with a rubber bung at either end. Air from a small pump was passed through the apparatus at the rate of 1 litre per minute ; this prevented condensation on the glass surface and helped to prevent any building-up in concentration of the vapour phase of any chemical used in the experiments. The films were prepared on pliable material. This was first laid out flat, coated with a deposit and then rolled into a cylinder to fit the tube. Where a glass surface was required, three glass rings just fitting the tube were used.

Ten bees were used in each chamber. Later in the experiments, the open-ended test chamber tubes were replaced by specimen tubes of which the ends were blackened to prevent phototropic effects. Tests with smoke indicated that the whole interior of the tubes was being sufficiently aerated. Bees confined in either form of tube did not normally fly but ran over the surface of the films ; under the influence of the poison, however, they occasionally became violently active.

Humidity control was achieved by bubbling the air through large wash bottles containing different solutions ; glycerol-water mixtures (Johnson, 1940) were used for high humidities and dilute sulphuric acid for the lower ranges ; in the latter cases, plugs of cotton wool were used to remove acid spray. The humidity was measured using the dew point hygrometer shown attached to the apparatus in fig. 1. This method of humidity control and measurement was found to be very successful as little variation took place over periods of 24 hours.

Temperature control was obtained by placing the whole apparatus, except for the air pump, in a large incubator having a glass door for inspection purposes. A large Winchester quart bottle was filled with fibrous asbestos, the air being passed through this before entering the wash bottles. The large warm surface area thus obtained facilitated a rapid rise in temperature. The air was circulated through this apparatus until the temperature of the thermometer within the hygrometer equalled that of the incubator. Successive dew point readings were taken until a constant equilibrium of humidity had been reached.

Preliminary tests showed that under what appeared to be identical conditions the point of complete immobilisation was very variable and difficult to detect. Affected bees would often struggle for hours on the surface of the film and any accumulation of bees would almost certainly result in local wetting of the film. A far more satisfactory measure of toxicity was found to be the point when 50 per cent. of the bees became so affected that they fell over on their backs and were unable to control their legs, *i.e.*, 50 per cent. knockdown.

A 1 per cent. emulsion of DNOC and a 1 per cent. (acid equivalent) solution of sodium DNOC were used. The films were prepared by dipping the surfaces to be treated into the emulsion or solution and allowing them to dry as evenly as possible. Where filter paper was used it was found necessary to dip a larger piece than was required, from which the uneven deposits at the edges were trimmed off.

(*a*) *Effects of varying humidities on the toxicity of films.*

Two series of films were prepared as described above on strips of cellulose acetate. Three chambers were used, two with identical films and one with the control bees. The incubator was maintained at 30°C. and the humidity was varied in each test. The results of the first series of tests using films of sodium salt are shown in Table II.

TABLE II.

Effect of relative humidity on toxicity of sodium salt.

Relative humidity	50% knockdown on films	Controls
30 per cent.	3 hrs.	3 hrs. 5 mins.
80 per cent.	2 hrs. 25 mins.	2 hrs. 45 mins.
89 per cent.	2 hrs. 30 mins.	2 hrs. 35 mins.
99 per cent.	35 mins.	2 hrs. 40 mins.

In the last test owing to the high humidity, moisture condensed on the surface of all the tubes. In all the other tests there was no significant difference in behaviour between the bees on the films and the controls. It appeared that the sodium DNOC only became effective when the film was actually wet.

The results of a second series of tests using acid DNOC are shown in Table III.

TABLE III.

Effect of relative humidity on toxicity of acid DNOC.

Relative humidity	50% knockdown	
0 per cent.	18 mins.	All the controls were unaffected for 2 hours after which the experiment was discontinued.
18 per cent.	26 mins.	
70 per cent.	18 mins.	
80 per cent.	25 mins.	
99 per cent.	15 mins.	

Moisture again condensed on the films at 99 per cent. relative humidity. This series of tests showed that, when films of the acid are used, the action of the poison is relatively independent of the moisture conditions and is active over a wide range of humidities.

(*b*) *Effect of varying the temperature on the toxicity of the films.*

Three of the test chambers were kept outside the incubator at a room temperature of 21°C. and three inside at 30°C. Humidity was kept at 20 per cent.

TABLE IV.

Effect of temperature on toxicity of DNOC and its sodium salt.

	Time for 50 per cent. to be affected at 20 per cent. R.H.	
	At 21°C.	At 30°C.
Film of sodium DNOC ...	203 mins.	182 mins.
Film of acid DNOC... ...	22 mins.	19 mins.
Controls	196 mins.	210 mins.

The results shown in Table IV confirm the first series of tests which indicated that the sodium salt was relatively ineffective as a dry film as compared with the acid DNOC and that a difference of 9°C. had only a small effect on the toxicity of the films of the sodium salt and no significant effect on the film of the acid. This also confirms Pradhan's observations using *Tribolium castaneum.*

(*c*) *Effect on toxicity of three different surfaces for the films.*

The three films selected were glass, cellulose acetate and filter paper, giving a range of surfaces from almost non-absorbent to highly absorbent. The incubator was maintained at 30°C. and air circulated at 10 per cent. relative humidity.

TABLE V.

The effect of three different surfaces on the toxicity of the acid.

Surface	Period for 50 per cent. to be affected	Controls
Glass	19 mins.	All lived for 2 hours after which the experiment was discontinued.
Cellulose acetate	21 mins.	
Filter paper ...	22 mins.	

The results shown in Table V indicate that there was no difference in toxicity, but it must be borne in mind that the weights of the deposit on each material are not comparable.

Using the same surfaces, the above tests were repeated at three different humidities at 30°C. and the results are shown in Table VI.

At 100 per cent. relative humidity all the films were wet before the bees were introduced.

The results indicate that with the sodium salt the surface of the films does affect toxicity and that filter paper is a far less toxic surface than either glass or cellulose acetate at 100 per cent. humidity. The data also indicates that a wet film of the

TABLE VI.

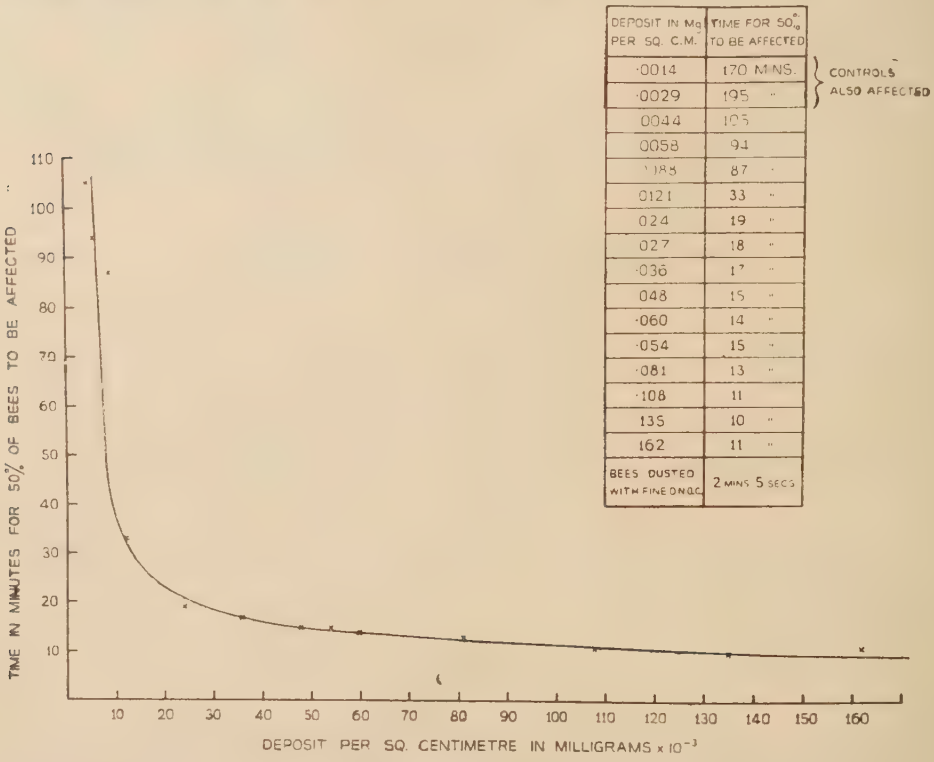
The effect of different surfaces at different humidities on toxicity of the sodium salt.

Relative humidity	Time for 50 per cent. of bees to be affected on :			
	(*a*) Glass	(*b*) Cellulose acetate	(*c*) Filter paper	(*d*) Controls
6 per cent.	180 mins.	170 mins.	225 mins.	220 mins.
90 per cent.	65 mins.	90 mins.	215 mins.	243 mins.
100 per cent.	20 mins.	22 mins.	182 mins.	265 mins.

sodium salt on either glass or cellulose acetate is as toxic to the bees as a dry film of the acid. It would appear that damp filter paper does not provide the wet film that is required for the sodium salt to be effective. At a humidity of 90 per cent. condensation took place during the experiment and, as the actual point was not determined, it may be assumed that the films on cellulose acetate and glass became toxic after the moisture had been deposited on the surface.

(*d*) *Determination of data relevant to the minimum toxic deposit of the acid DNOC.*

In this case, in order to simulate field conditions, the films were deposited on cabbage leaves. The films were prepared in a settling mist tower as described by



DEPOSIT IN Mg PER SQ. C.M.	TIME FOR 50% TO BE AFFECTED
·0014	170 MINS.
·0029	195 "
0044	105
0058	94
0088	87 "
0121	33 "
024	19 "
027	18 "
·036	17 "
048	15 "
·060	14 "
·054	15 "
·081	13 "
·108	11
135	10 "
162	11 "
BEES DUSTED WITH FINE DNOC	2 MINS 5 SECS

CONTROLS ALSO AFFECTED

Fig. 2.—Relationship between weight of deposit of DNOC and time for 50 per cent. knockdown.

Way (1949), using the DNOC dissolved in benzene. Sheets of thin tinfoil were alternated with the leaves at the bottom of the tower and these could be weighed to determine what weight of deposit had fallen per square centimetre over the floor of the tower.

A range of deposits was prepared, two of each weight, and these were tested out as soon as they had dried. Only five bees were put in each tube in this experiment as transpiration by the cabbage leaf increased the risk of condensation of moisture on the film. A fairly brisk current of air was passed through the tubes and all the tests were carried out in the laboratory at an average temperature of 21°C. and a relative humidity varying from 55 per cent. to 70 per cent. The time taken for a 50 per cent. " knockdown " on the films was used as a measure of their toxicity.

The results obtained and the relationship between weight of deposit in mg. per sq. cm. and the time in minutes for 50 per cent. knockdown are shown in fig. 2. The curve which is at first asymptotic to the Y axis then rapidly becomes asymptotic to the X axis and this change takes place approximately between the deposits of 10×10^{-3} and 25×10^{-3} mg. of DNOC per sq. cm.

The above series of experiments shows that DNOC is a rapidly acting poison under a wide range of environmental conditions, whilst the sodium salt is apparently non-toxic as a dry film and requires the presence of a film of moisture to become effective. A wet film of the sodium salt is as rapid in toxic action as one of DNOC of equivalent concentration.

No provisions were made to feed the bees so that the results do not indicate whether prolonged contact with the sodium salt might be toxic, but the results of the contact spray tests indicate that this is unlikely. Initially, the DNOC appeared to increase greatly the activity of the honey bees and when they were placed on these films their activity would gradually increase for about 5 minutes by which time they would often be rushing about. Sometimes this would continue until they lost control and fell on their backs or at other times they would show periodic peaks of activity. Goble and Patton (1946) showed that sublethal doses of sodium DNOC when fed to honey bees increased their metabolic rate as indicated by changes in respiration.

The toxicity of the chemicals as stomach poisons.

An emulsion of DNOC and a solution of the sodium salt were prepared as before except that they were made up in an approximately 65 per cent. solution of sucrose.

Individual bees were fed with known doses of insecticides. They were starved for 1 hour, anaesthetised with carbon dioxide and then attached to glass rods using beeswax (Frings, 1944). On recovering, the tarsi of the bees were stimulated with a sugar solution and this resulted in the erection of the mouth-parts which were then inserted into the end of an " Agla " micrometer syringe. The micrometer screw

TABLE VII.

The toxicity of the acid and salt as stomach poisons.

Wt. of toxic material fed to each bee	Percentage kill	
	Using DNOC	Using sod. DNOC at equivalent acid concentrations
·005 mg. ...	100	100
·0025 mg. ...	65	55
·0010 mg. ...	40	45
·0005 mg. ...	33	20
·0001 mg. ...	0	5
Controls ...	5	0

was gradually turned as the bee fed so as to keep the liquid flush with the tip of the syringe and 1/100 ml. was fed to each bee. After feeding, the bees were caged separately so as to prevent them from feeding each other. Control bees were handled to the same extent and fed with plain syrup.

At least 20 bees were fed at each concentration, but unless several operators can be employed the technique is very laborious.

The results in Table VII show that there is little difference between the two chemicals as stomach poisons. Most of the deaths occurred within 30 minutes of being fed.

Penetration of beeswax by acid DNOC and sodium DNOC.

It was assumed that the differences in toxicity of the acid and salt observed in the above experiments were due to differences in their capacity to penetrate the bee's cuticle. The following experiments were carried out to provide evidence in support of this assumption. Beament (1945) and others have used beeswax in the preparation of artificial membranes comparable with the lipoid layer of an insect's epicuticle.

Several sections of pure beeswax 2×1 cm. and 15 μ in thickness were prepared using a microtome. They were laid out on white filter paper, and a heap of approximately ·05 gm. of either the acid or the salt was placed on alternate sections. After 6 hours had elapsed, the sections were carefully lifted from the paper and under those sections which had borne the DNOC a pronounced yellow stain was apparent but no staining was visible with the sodium salt. This shows that only the acid is capable of penetrating a wax section in the dry state.

The above experiments were repeated using a suspension of DNOC (prepared by adding a solution of DNOC in acetone to a dilute solution of gelatin) and a solution of the sodium salt, each at a concentration of 0·5 per cent. After 4 hours at room temperature, examination showed that the drops had evaporated and that penetration had only occurred in the case of the DNOC.

In order to prevent the evaporation which occurred in the last experiment special cells were made. A piece of fine muslin was fastened over the end of a piece of glass tubing 0·6 cm. in diameter and 4 cm. long. The muslin was impregnated with beeswax by successive dippings into a solution of beeswax in carbon tetrachloride (Webb & Green, 1945). In this way a watertight cell was prepared.

The cells were clamped down on to wet filter paper and ·5 ml. of either the DNOC suspension or sodium salt solution used in the previous experiments was introduced. Six cells were used with each chemical. After 4 hours, examination of the filter paper underlying the wax membrane revealed a distinct stain in all cases showing that penetration had occurred.

The experiment was repeated using the ammonium salt of DNOC and penetration of the wax again occurred in under 4 hours.

General Discussion of Laboratory Experiments.

In the solid state it may be expected that DNOC would consist of a lattice work of un-ionised DNOC molecules. In solution, a cresol would be a weak acid but the substitution of the two nitro groups into the nucleus would facilitate the loss of hydrogen from the hydroxyl group and thus increase the strength of the substance as an acid. This is indicated by the dissociation constant given by Krahl and Clowes (1938) to be $4{\cdot}4 \times 10^{-5}$ and therefore a comparatively large concentration of the acid anions would be present in solution. The sodium salt is a strong electrolyte completely dissociated in solution and in the solid state the substance will be an ionic latticework of sodium and DNOC ions.

In the above experiments DNOC was shown to be highly toxic to the honey bee in aqueous medium, as a dry film and as a stomach poison. Changes in environment seemed to have little effect on toxicity.

The sodium salt was toxic in aqueous solution as a contact poison, and when fed to the bees. The toxicity of aqueous sprays appeared to be dependent on the humidity of the environment after spraying ; this influenced the time which the spray took to dry on the cuticle. The higher the humidity the longer the time taken to dry.

As a residual film the sodium salt was toxic only when it passed into solution. The time for " knock-down " on the wet filter paper was much longer than on the other two surfaces, and this suggests that the cuticle must be bathed in the solution before penetration can occur.

These observations, together with similar effects of the two chemicals as stomach poisons, suggest that the cuticle can act as an effective barrier against the penetration of the sodium salt in the dry state. From the work of Beament (1945) and others on the wax waterproofing layer of the epicuticle it seems likely that it is this layer which is the actual barrier. The presence of such a lipoid layer on the epicuticle of the honey bee has not been described, but G. D. G. Jones (unpublished 1950) has shown that the abrasion of the bee's cuticle with alumina dusts is followed by a rapid loss of moisture.

The solubility of various solutes in solvents of low dielectric constant is largely dependent upon their ionic condition. The greater the polarity of a solute then the lower its solubility in such a solvent. It is therefore probable that the penetration of the DNOC is due to the solubility in the wax of the un-ionised weak acid molecules, and that the ionised salt does not penetrate when dry because of its lower solubility in the solvent.

The toxicity experiments and the tests with wax membranes all showed that the sodium salt could penetrate in aqueous solution. It was thought that the solubility of the sodium DNOC in the lipoid layer or beeswax might be due to a slight hydrolysis taking place in the salt solution, and the resulting free sodium hydroxide having an emulsifying action on the wax. This view was not upheld by the observation that the ammonium salt was also capable of penetrating the wax membrane, though it is conceivable that substances having the structure of these salts may of themselves have an emulsifying action on wax when in aqueous solution.

To conclude, it must be stated that whilst a tenable explanation of the differing toxicities of the acid and salt in the dry state has been offered, the capacity of the sodium salt to penetrate in aqueous solution still remains unexplained.

Field Experiments.

The graph (fig. 2) based on data relative to the minimum toxic deposit of the acid shows that a film on a leaf surface (cabbage) as judged by the rate of paralysis, rapidly becomes more effective when the deposit is increased from 0·010 mg. to 0·02 mg. per sq. cm., further increases resulting in little change in the rate of knockdown. Under field conditions approximately 6 lb. of the pure acid is applied per acre for use as a herbicide. This gives a maximum deposit of 0·066 mg. per sq. cm. but even allowing for run-off from leaf surfaces and floral parts, it would seem likely that a deposit in excess of 0·010 mg. per sq. cm. would remain. It would thus appear that continued foraging by bees on these surfaces would prove toxic.

Attempts to estimate this effect under field conditions using small plots were inconclusive owing to the unpredictable behaviour of the foraging bees and they were abandoned for the large scale experiment described below.

A twenty-acre field of spring oats (*Avena sativa*) bearing a very heavy infestation of charlock (*Sinapis arvensis*), the latter smothering the growing cereal, was used for the experiment. The flowers began to open on 13th May and this coincided with the beginning of a period of very warm weather. By 16th May nearly all the plants had open flowers and two weighed hives, each having bees covering 10 British Standard brood frames were placed on the edge of the field. At this time a few honey bees were seen on the crop, all of a dark-coloured strain, but by the following day yellow-banded bees similar to those imported were found on the crop near to the hives and in another 24 hours they had spread over the whole field. Occasionally individuals of other strains were seen on the crop but rough estimates showed that over 80 per cent. of all the bees seen were of the yellow-banded strain. Approximately 100 of these were marked in the field and very soon afterwards marked bees were seen entering and leaving the hives.

With the exception of one acre of brussels sprouts (*Brassica oleracea* var. *gemmifera*) in full bloom about ⅓rd of a mile away, no other crops yielding nectar could be found within a ¾-mile radius.

Spraying commenced at 10.00 a.m. on 19th May and at this time an approximate estimate of the foraging population in the field was made by observing on what area at least one bee could be seen foraging at any given time over the field.

The part of the field nearest the hives was more heavily populated, with approximately 1 bee per sq. yard. This was estimated by pacing out this area and observing how many bees could be seen in that area at any one time. At the end of the field furthest from the hives one had to search for a foraging bee ; a very approximate average estimate over the whole field was one bee in every four square yards, which gives a total foraging population of about 24,000. The population of bees within the hives was roughly assessed at 60–70,000 workers.

The material used was the acid DNOC specially obtained for the experiment as a 50 per cent. paste containing a suspending agent. One gallon of this was added to 100 gallons of water, this being sufficient for the spraying of one acre.

The part of the field nearest the hives was sprayed first and 15 acres were completed the first day.

The following is a description of a typical sequence of events on an acre of sprayed charlock :—

10.30 a.m.	Area very heavily worked by bees. Spraying commenced. The spraying machine seemed to disturb some of the bees but not all—some were hit by the spray.
10.35 a.m.	Whilst the spray was wet, sporadic visits were made to the flowers, the bees barely touching the flowers before flying off.
10.45 a.m.	Spray dry. Quite a number of visits—more than when foliage was wet. Spray material appeared to have some repellent effects. The flowers ceased to be attractive as slight wilting had taken place.
11.05 a.m.	A very occasional moribund bee seen clinging to a leaf and very few bees seen in sprayed area.
12.30 p.m.	Slight shrivelling of sprayed blossom—no visits.
1.15 p.m.	Blossom quite shrivelled ; only a very occasional visit by a pollen-gathering bee.

Large white trays were put on the ground in front of the hives and these were kept under observation whilst spraying was in progress. Affected bees began to arrive 20 minutes after spraying had commenced, never more than two at a time. Some gained the hives and were later either dragged out and landed on the tray or were flown out well clear of the hive ; the latter rarely fell on the tray. Others, on arriving from the field, landed on the tray and flew away again, making no effort to regain the hive. The symptoms of affected bees were staggering and inability to fly properly. In the first 3 hours a total of 78 dead bees collected on the trays in front of the hives. By 2.30 p.m. about 12 acres had been completed and it was noticed that the population of bees working the unsprayed part of the field was much smaller than during the morning. The temperature at 12 noon was 70°F. and it rose to a peak of 74°F. about 2·0 p.m. Fifteen acres were sprayed by 4·30 p.m. and the remaining 5 acres were finished the following morning when the temperature had dropped to 54°F. and no foraging took place.

The hives were opened and a detailed examination was made before and after the experiment and no obvious loss of flying bees could be detected. In both hives the eight frames of brood were well-covered with bees. The hives were left on the site for 3 weeks and both gained in weight.

Discussion.

The fall-off in numbers of foragers from 3 p.m. is a commonly reported observation when bees are working charlock on hot days : nectar secretion appears to reach a peak before noon and falls off afterwards. It may have been that the DNOC had tended to repel the bees from the whole crop but it is considered improbable that the fall off in numbers on the unsprayed portion was related to the spraying. Some loss of flying bees definitely did occur but the repellent effect of the spray in solution followed by the wilting and shrivelling effect when dry, makes sprayed flowers unattractive to bees. The higher the temperature the greater the wilting and herbicidal effect, whilst below a certain temperature the bees will not forage, and this combination of factors makes it unlikely that bees will continue active foraging on treated plants. On the second day wilting and shrivelling took much longer ; but no foraging took place.

It is conceivable that under different conditions greater losses might occur but it is unlikely that hives will normally be in such close proximity to an isolated field of charlock. The charlock was exceptionally dense—a rough indication being that it was almost impossible to tread anywhere on the field without touching a charlock plant, and such infestation is again very exceptional.

Observations in France during 1947 (Chancogne & others, 1948) on the use of DNOC to control charlock, showed that only the foragers coming from hives very near the treated fields were killed, but the mortality did not extend to either the brood or young bees in the hive. The hives were seriously affected but not destroyed and after a period of fine weather the colonies quickly regained their original strength. These observations are in general agreement with the present ones except that a more noticeable loss of flying bees occurred in the former.

Summary.

Laboratory and field experiments were carried out to study the toxicity of 3 : 5 dinitro-ortho-cresol and its sodium salt to the honey bee.

The acid DNOC was shown to be a rapidly acting poison under a wide variety of conditions and its toxicity was not greatly affected by differences in temperature or humidity during or after treatment.

Although both the acid and salt were equally toxic as stomach poisons, considerable differences were observed between the two substances as aqueous sprays and dry films. The toxicity of the sodium salt as an aqueous spray was considerably influenced by the humidity of the environment after spraying ; the higher the humidity the greater the kill.

The sodium salt was apparently non-toxic as a dry film and increasing the humidity of the environment had no effect until the saturation point was reached and the salt went into solution. At this point the salt was almost as rapid in action

as the acid. The type of surface on which the film was deposited was also shown to affect the toxicity.

Experiments were carried out on the penetration of the two substances through beeswax and these confirmed that whilst the acid could penetrate the beeswax in all forms tested the salt would only penetrate in aqueous solution.

The effects of the acid DNOC on a population of foraging bees when used as a herbicide to control charlock in a 20-acre field of spring oats was investigated. It was shown that whilst the population of foraging bees was reduced no appreciable damage was inflicted on the colony. It is considered that at temperatures when active foraging on charlock takes place, spraying with DNOC will be followed by a rapid wilting of the flowers which will render them unattractive as sources of nectar or pollen.

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NOTE ON DAMAGE TO GRAZING BY GRASSHOPPERS IN KENYA.

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Widespread and severe damage to grass in Kenya is caused from time to time by several species of locusts, which have outbreak centres outside the country. Severe damage by indigenous grasshoppers, however, seldom occurs. For this reason it is considered of interest to record an increase in population of several species of indigenous grasshoppers to a level which caused serious damage to grazing in a limited area of Kenya in 1950. This, as far as is known, is the first recorded instance of a possible hazard through grasshoppers, to the development of ranching in the grasslands of East Africa. The matter was first brought to my notice in July 1950 by Mr. Byng Hall of Soysambu Estate, Elmenteita, who stated " we are suffering from a plague of grasshoppers—they cover several thousand acres and have stripped the leaf off several hundred acres of grass ".

A few days after receipt of this letter I visited the area with Dr. B. P. Uvarov and we found that there was indeed a high population of grasshoppers consisting of many species and genera and totalling a good many to the square yard as indicated by the fact that they were taken in numbers by every sweep of the net.

The area infested was near Lake Elmenteita in the Rift Valley. The major vegetation community covering a large area of the Rift Valley and of the southern part of Kenya is the Scattered Tree Grassland : *Acacia-Themeda*. The actual area in which the grasshoppers were found was a part of an association within this community being the ancient lake bed resulting from a former extension of the Rift Valley lakes including Lake Elmenteita nearby. This association is strongly dominated by the grasses, *Cynodon dactylon* Pers. (Common Star Grass) and *C. plectostachyum* Pilger (Naivasha Star Grass), with a mixture of other grasses and shrubs, and may be considered as a sub-climax, occurring as a result of the particular soil. In recent years there has been a tendency for *Aristida keniensis* Henrard to invade the area, which tendency has no doubt been accentuated by periods of severe drought. These species of grass are at present the dominants in the area.

In the more ancient parts of the old lake bed further away from, or higher than, the present lakes the association consists of the shrub, *Tarchonanthus camphoratus* L. (known as Ol-leleshwa in the Masai language), and the *Cynodon* species.

Collecting was done in a low area not much above the level of Lake Elmenteita and also at a slightly higher level on a slope leading down to the lower area, on which slope *T. camphoratus* was in evidence. At the time of the first visit there was a little difference in the species of grasshopper found in these two areas but the lower area had the higher population. The species present in largest numbers and which appeared to be responsible for the bulk of the damage were *Gastrimargus brevipes* Sj., and *Caloptenopsis glaucopsis meruensis* Sj. and in one area *Gastrimargus* was present in every square yard. The infestation had almost completely stripped the grass resulting in almost bare soil and it was considered dense enough to warrant baiting. A bran and BHC bait was laid later with reported good results. Apart from the two species of insects mentioned there were many other Acridids present as is shown in the following list :—

	July	December
**Cataloipus fuscocoeruleipes* Sj.	A H	—
**Gastrimargus brevipes* Sj.	A	—
**Caloptenopsis glaucopsis* (Wlk.) subsp. *meruensis* Sj.	A H	A
**Caloptenopsis speciosus* Sj.	H A	A
Platyphymus granulatus Uvarov	A H	A
**Afrohippus* sp.	A H	A
Eyprepocnemis sp.	A	H
**Pnorisa squalus* St.	—	A
**Rhaphotittha meruensis* Sj.	A H	—
Paracomacris sp.	A	A
**Gymnobothrus* sp.	A	A
Acrotylus elgonensis Sj.	A	A H
Cyrtacanthacris tartarica (L.)	A	A
Acrida sp.	A H	A
Parasphena sp.	A	A
Orthochtha sp.	—	A

* Species marked thus were numerous.

A=adults, H=hoppers.

A further visit was paid to the site in December 1950 when I was accompanied by Miss Z. Waloff. We collected again over the same areas and substantially the same species were present as is shown in the list, but no longer in large numbers. In fact instead of the large numbers which were taken in a few sweeps of the net in July, the insects were very scarce and had to be tracked down and caught singly. *Gastrimargus* was not in evidence at all, although one specimen was found in the collection later, and *Caloptenopsis* was rare, the largest number found to rise in 15 paces was three, and the average in 15 paces less than one. It may be taken that the average population was under one in 30 sq. yds.

It is certain that this outbreak of grasshoppers in the area was unusual since Mr. Byng Hall stated that he had never in 20 years there seen such an increase. The average annual rainfall on Soysambu over the past 11 years since 1940 was 25 ins. whereas the rainfall in 1949 was 21·68 and in 1950 was 18·68 only, these two years being the driest since 1933–34. A peculiarity resulting from the distribution of rainfall in 1950 may be mentioned, as conceivably having an influence on the multiplication of grass-feeding insects. I give this in Byng Hall's words, " this year (1950) has been not only very dry but rain has come in patches, *i.e.*, the grass turned green, dried off, turned green etc. repeatedly. This was particularly true of the area which was most heavily infested and I think the change from dry to green took place perhaps four or five times at least in that area."

In May and June of 1950 an unusually heavy infestation of grass by several species of leaf-eating Coleoptera, especially the Coccinellid, *Epilachna hirta* (Thnb.) occurred over a wide area of the Rift Valley and was especially severe on Cole Estates Kekopey Gilgil, a farm adjacent to Soysambu. This attack which did much damage to grass over an area of many thousands of acres was unusually severe. It is conceivable that the distribution of rain in the area was a factor in the development of this high population also.

Summary.

A development of grasshoppers to minor plague proportions over a limited area of the Rift Valley near Lake Elmenteita occurred in 1950. The two chief species concerned were *Gastrimargus brevipes* Sj. and *Caloptenopsis glaucopsis meruensis* Sj. but many other genera and species were present and are listed. The distribution of

rain with appreciable falls followed several times by dry spells may have been a factor contributing to the increase. An unusual increase of the Coccinellid, *Epilachna hirta* (Thnb.) also occurred in the area a month or two before.

Acknowledgements.

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I owe many thanks to my colleague Mr. D. C. Edwards for the ecological description of the area. Also to Miss Z. Waloff for assistance in observations on the second visit.

R

STUDIES OF BRITISH ANTHOMYIID FLIES.

By Mary Miles.

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(Plate V.)

III. Immature Stages of *Delia cilicrura* (Rond.), *D. trichodactyla* (Rond.), *Erioischia brassicae* (Bch.), *E. floralis* (Fall.) and *Pegohylemyia fugax* (Mg.).

The immature stages of *Delia cilicrura* (Rond.), *D. trichodactyla* (Rond.), *Erioischia brassicae* (Bch.), *E. floralis* (Fall.) and *Pegohylemyia fugax* (Mg.) occur separately or in mixed populations on cruciferous crops, and since they differ in habit and importance it is advisable that their various stages should be recognised and distinguished. *E. brassicae* and *E. floralis* are true cabbage root flies and are widely distributed on cruciferous crops in Northern Europe, North America and parts of Asia. *D. cilicrura* and *D. trichodactyla*, the bean seed flies or seed corn maggots, are primarily scavengers on plant and animal matter in the soil ; they are found at the roots of cruciferous crops in association with *E. brassicae* and *E. floralis* (Lundblad, 1933 ; Fulton, 1942 ; Miles, 1948 ; Brooks, 1949) and they occur alone on crucifers set out in September and October (Miles, 1948). *P. fugax* is associated with decaying vegetation, and from May to October its eggs are numerous on cruciferous crops (Miles, 1950).

Egg Stage.

The eggs of the several species have a common basic pattern. They are white, elongate, with one side convex and the other side slightly concave, rounded posteriorly and truncated anteriorly where there is a thick rim round the micropylar area. The chorion has a sculptured surface, the pattern of which tends to vary with the species, and there is a smooth white vitelline membrane which can be seen when the chorion is torn.

Eggs of *D. cilicrura* (Pl. V, fig. 1) have a finely reticulated surface, the pattern being dominated by the broken, longitudinal ribbing. A pair of thick ridges arise in the anterior rim and extend along the concave side for about one-fifth of the length (one of the ridges is visible on the egg on the left in Pl. V, fig. 1). A series of 35 eggs had an average length of 0·92 mm. (range 0·9–0·95 mm.). It has not been possible to separate eggs of *D. cilicrura* from those of *D. trichodactyla.*

Eggs of *E. brassicae* (Pl. V, fig. 3) have a coarse, longitudinal ribbing on the chorion, thicker and less broken than that on the chorion of *D. cilicrura.* A pair of thick ridges arise in the anterior rim and extend along the concave side to the tip where they meet. The area between the ridges is more delicately sculptured and is ruptured at eclosion. Measurements showed that the length of the eggs varied from 0·9 to 0·95 mm., with an average of 0·93 mm.

Eggs of *E. floralis* have the pattern of the chorion similar to that of eggs of *E. brassicae* but are distinctly larger (Pl. V, fig. 4) ; the length varies from 1·1 to 1·2 mm., with an average of 1·16 mm. Vodinskaya (1928) records the length of eggs of *E. floralis* as 1·2–1·5 mm.

Eggs of *P. fugax* (Pl. V, fig. 2) have the chorion distinctly reticulated, the cells being large and rounded. A pair of irregular, keeled ridges arise in the micropylar rim where they form small shoulder-like projections and extend along the concave side to the apex where their junction forms a blunt tip. Eggs of *P. fugax* had an average length of 1·06 mm.

Larval Stage.

Larvae of the several species are typical legless maggots with the head reduced and the posterior tip of the body somewhat triangular in profile, with a distinct apical ridge separating the dorsal oblique area (Cameron, 1914) which bears the posterior spiracles, and the ventral truncated area (Cameron, 1914) which bears the anus. They have fleshy conical or sub-conical protuberances or tubercles on the dorsal and ventral areas of the 8th abdominal segment, those associated with the dorsal oblique area and the apical ridge forming what is commonly called the corona. They vary in length from *D. cilicrura* and *D. trichodactyla*, which are 6–7 mm. when fully grown, to *E. floralis* which attains a length of 9—10 mm. *E. brassicae* and *E. floralis* have stout larvae with the prothorax almost as broad as the rest of the body, the larvae of *P. fugax* are very slender anteriorly and attain their maximum breadth in the 7th and 8th abdominal segments ; larvae of *D. cilicrura* and *D. trichodactyla* are intermediate between the stout larvae of *E. brassicae* and *E. floralis* and the slender larvae of *P. fugax*. The cuticle of the larva of *P. fugax* differs from that of the other species in being closely but irregularly covered with minute transparent spicules.

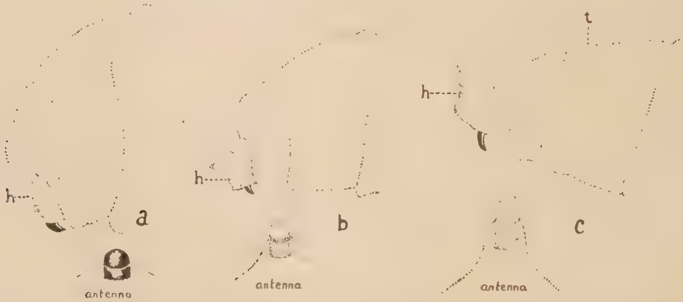


Fig. 1.—Profile of head (h) and prothorax (t) of a, *E. brassicae* (×27) ; b, *D. cilicrura* (×33) ; c, *P. fugax* (×27).

Head.—In the several species there are marked differences in the size relationships between the head and the prothorax and in the degree of development of fleshy lateral lobes bearing the antennae and maxillary palps (fig. 1). In *E. brassicae* and *E. floralis* the head is deeply retracted into the broad prothorax and the antennae and maxillary palps are carried on small lateral swellings or lobes. The cuticle surrounding the mandibles is heavily sclerotised. In *D. cilicrura* and *D. trichodactyla* the head is partly retracted into the prothorax, but is relatively larger and more conspicuous than in the preceding species owing to the increased development of the lateral lobes, which gives the head a deep median cleft. As in *E. brassicae* the cuticle round the mandibles is sclerotised in transverse ridges. In *P. fugax* the head, though retractable, is usually exerted from the relatively narrow prothorax, and the lateral lobes are so enlarged that the head appears almost cleft into two parts. The cuticle round the mandibles has broken transverse sclerotised ridges.

Antennae.—The antennae form the dorsal tips of the lateral lobes and consist of a sclerotised basal ring, more or less embedded in the head, and a free terminal segment. Differences in the form of the antennae in the several species appear to be associated with the development of the lateral lobes. In *E. brassicae* and *E. floralis* the basal ring is heavily sclerotised and clearly visible beneath the cuticle ; the terminal segment is almost globular and also heavily sclerotised. In *D. cilicrura* and *D. trichodactyla* the basal ring and the terminal segment are less intimately associated and less heavily sclerotised than in the preceding species, and the terminal segment is more elongate. In *P. fugax* the greater development of the lateral lobe has further dissociated the basal ring and the terminal segment of the antennae, sclerotisation is further reduced and the terminal segment further elongated (fig. 1).

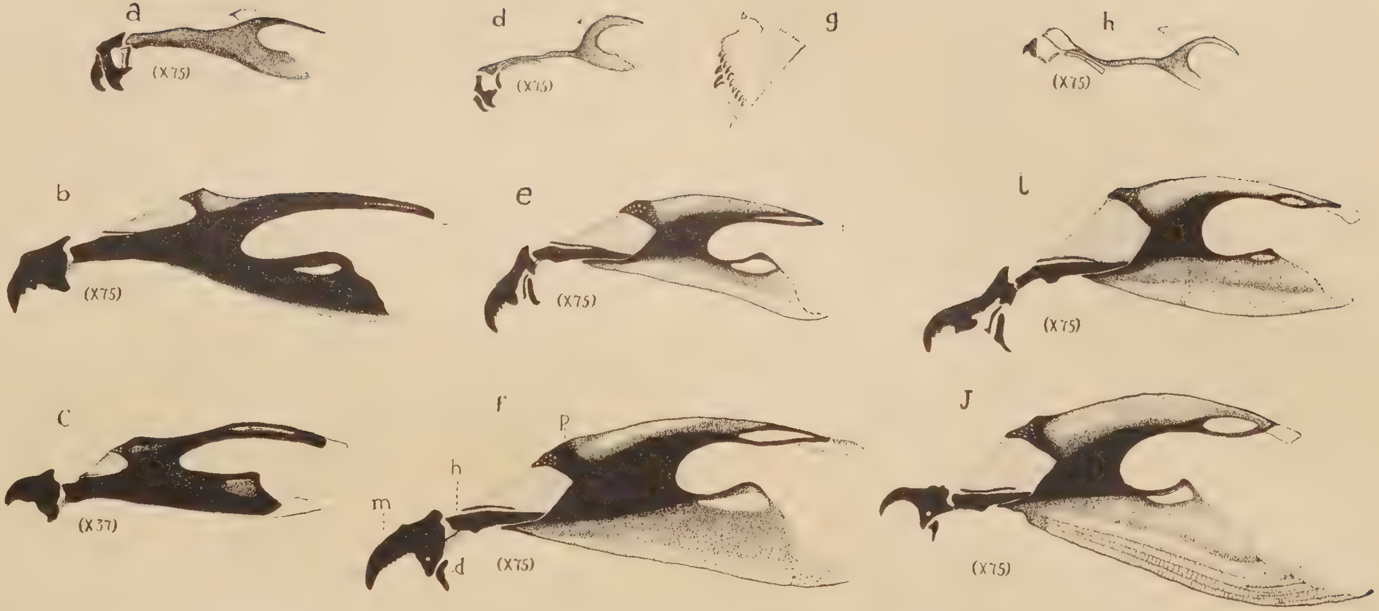
Maxillary palps.—The maxillary palps form the ventral tips of the lateral lobes and each palp consists of a sclerotised ring approximately similar to the basal ring of the corresponding antenna and, like it, is also embedded in the head. Within the ring are 4–5 finger-like processes, two of which are more heavily sclerotised than the rest. As with the antennae, sclerotisation is most marked in *E. brassicae* and least developed in *P. fugax*.

Mouth-parts.—The bucco-pharyngeal armature shows characters that can be used to distinguish instars and to contribute to the separation of species, but in all three instars that of *E. brassicae* is similar in form to that of *E. floralis* and that of *D. cilicrura* to that of *D. trichodactyla*.

In the first instar each mandible of *E. brassicae* (fig. 2, *a*) consists of two stout crochets ; the anterior crochet articulates with the basal crochet which has stout ventral and dorsal processes. The hypostomal and pharyngeal sclerites are fused and rather heavily sclerotised. In *D. cilicrura* (fig. 2, *d*) the buccal armature of the first instar is lightly sclerotised. Each mandible consists of two separate slender crochets and associated with them is a series of 10–11 cuticular spines on each side of the face (fig. 2, *g*). The hypostomal and pharyngeal sclerites are fused. In *P. fugax* (fig. 2, *h*) the mandible of the first instar has only one crochet. The arms of the hypostomal sclerite are broad and membranous and united with the deep, membranous pharyngeal sclerite.

The buccal armature of the second instar differs from that of the first. In *E. brassicae* (fig. 2, *b*) the mandible is short and stout and with two teeth on its ventral surface. The hypostomal and pharyngeal sclerites are fused and heavily sclerotised. In *D. cilicrura* (fig. 2, *e*) the mandible is long and slender with four small teeth on the vental surface and two accessory sclerites associated with the postero-ventral process. The hypostomal and pharyngeal sclerites are distinct and less sclerotised than those of *E. brassicae*. In *P. fugax* (fig. 2, *i*) the mandible resembles that of *D. cilicrura* but has only two teeth on the ventral surface. The hypostomal and pharyngeal sclerites are distinct and less sclerotised than in either of the preceding species.

The buccal armatures of the third instar show further changes. In *E. brassicae* (fig. 2, *c*) the stout mandibles have no teeth on the ventral surface, the hypostomal and pharyngeal sclerites are fused, and the pharyngeal sclerite is long, rather narrow and heavily sclerotised. In *D. cilicrura* (fig. 2, *f*) the third instar mandibles are shorter and stouter than those of the second instar and are strongly ridged on the ventral surface, the ridges appearing as a series of 14–15 deep serrations on the ventral surfaces of the developing mandibles just before the second ecdysis. The ventral process has one accessory sclerite and the hypostomal and pharyngeal sclerites are distinct, the pharyngeal sclerite being membranous dorsally and ventrally and the inner ventral surface showing faint longitudinal ridges. In *P. fugax* (fig. 2, *j*) the third instar has slender sickle-shaped mandibles, smooth on the ventral surface and having one accessory sclerite associated with the ventral process. The hypostomal and pharyngeal sclerites are distinct, the pharyngeal sclerite being deep and largely membranous with well developed longitudinal ridges on the inner ventral surface.


a
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p
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m
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(X75)
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Fig. 2.—Bucco-pharyngeal armature of first, second and third instars of a—c, *E. brassicae* ; d—f, *D. cilicrura* (g, exserted head showing cuticular spines of first instar of *D. cilicrura*) ; h—j, *P. fugax*.
(m, mandible ; h, hypostomal sclerite ; p, pharyngeal sclerite ; d, accessory sclerite.)

Anterior spiracles.—Anterior spiracles are present in the second and third instars and consist of finger-like processes spread fan-wise dorso-laterally at the junction of the pro- and meso-thoracic segments. The finger-like processes each with a terminal opening, are similar in the several species but their number, taken in conjunction with other characters, are of value in identifying the larvae. In *D. cilicrura* and *D. trichodactyla* the anterior spiracles have 5–8 processes ; in *E. brassicae* and *P. fugax* they have 11–13 processes, those of *E. brassicae* being more densely sclerotised ; and in *E. floralis* they have 14–16 processes.

Posterior spiracles.—The posterior spiracles are similar in form throughout the several species but they vary in the degree of sclerotisation, which is greatest in *E. brassicae* and least in *P. fugax*. In the first instar they are knob-like structures with a circular opening, projecting horizontally from the dorsal oblique area. In the second and third instars the knob-like character persists but is less obvious because the " stem " is fleshy. In *E. brassicae* the spiracular rim, including the eclosion scar, is heavily sclerotised ; in *E. floralis* sclerotisation is less developed and only the rim of the eclosion scar (Keilin, 1944) is sclerotised ; in *D. cilicrura*, *D. trichodactyla* and *P. fugax* the posterior spiracles are lightly sclerotised and the eclosion scar is indistinct.

Tubercles of eighth abdominal segment.—A conspicuous character of these larvae is the paired conical or sub-conical protuberances or tubercles on the eighth abdominal segment. Supplementary observations on *Pegomyia betae* (Curt.), *P. bicolor* (Wied.), *Hylemyia antiqua* (Mg.), *Leptohylemyia coarctata* (Fall.), *Chortophila seneciella* (Meade), *Delia brunnescens* (Zett.), and *Hylemyia echinata* (Séguy) show that although certain tubercle patterns recur, nevertheless the form and arrangement of the tubercles, taken in conjunction with other characters, are of value in the identification of species.

Other workers (Cameron, 1914 ; Gemmill, 1927) have illustrated the tubercle pattern of larvae and have numbered the paired tubercles but their systems of numbering have not been similar, and Brooks (1949) has identified the tubercles by means of letters. Since the positions of the tubercles are broadly similar in various species though some modification or suppression may occur, it is thought that names indicative of their positions might be more useful than numbers for comparative studies, and the following names are suggested (fig. 3) :

1. *dorso-central tubercles*, situated near the mid-dorsal line.
2. *dorsal tubercles*, often situated towards the anterior edge of the segment.
3. *dorso-lateral tubercles*, situated on the lateral margin of the dorsal oblique area.
4. *lateral tubercles* situated on the lateral area of the segment below the mid-lateral line.

5 and 6. *outer and inner apical tubercles*, usually forming the apical ridge of the segment.

7. *ventro-apical tubercles*, situated on the ventral truncated area near the apical ridge, below and between the inner apical tubercles.
8. *supra-anal tubercles*,* situated on the ventral truncated area near the anus.

The arrangement of the tubercles of the eighth abdominal segments of *D. cilicrura* and *D. trichodactyla* is shown diagrammatically in fig. 3 *a*. This is the simplest pattern that has so far been observed in the Anthomyiid flies. It occurs also on larvae of *Hylemyia antiqua*, and *Chortophila seneciella*. In *D. cilicrura* the dorso-central, dorsal, dorso-lateral, lateral and supra-anal tubercles are approximately the same size ;

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*This pair of tubercles is not homologous with the anal " false feet " on the " anal area ", probably the remains of ninth abdominal segment, of *Calliphora erythrocephala* (Mg.), (Lowne, 1890), *Lucilia sericata* (Mg.) and *Muscina assimilis* (Fall.) (Muscidae).

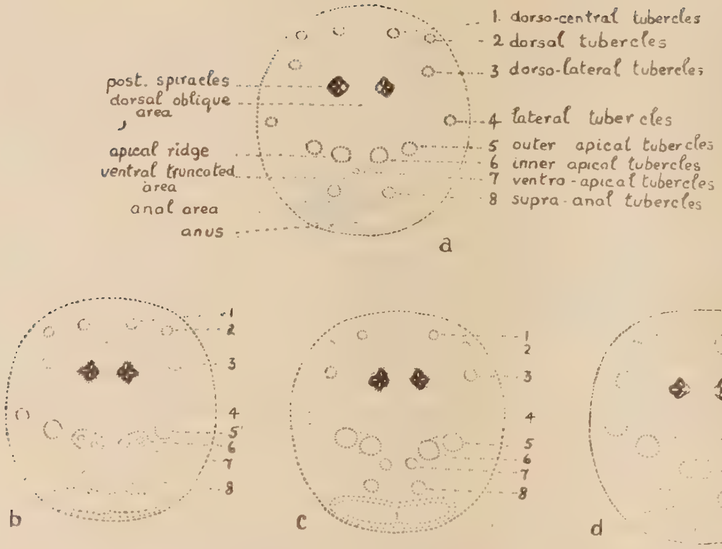
1. dorso-central tubercles
2 dorsal tubercles
3 dorso-lateral tubercles
4 lateral tubercles
5 outer apical tubercles
6 inner apical tubercles
7 ventro-apical tubercles
8 supra-anal tubercles
post. spiracles
dorsal oblique area
apical ridge
ventral truncated area
anal area
anus
a
b
c
d
1
2
3
4
5
6
7
8

Fig. 3.—Posterior view (diagrammatic) of tip of abdomen of larva of a, *D. cilicrura*; b, *E. brassicae*; c, *E. floralis*; d, *P. fugax*.

the outer and inner pairs of apical tubercles are larger, the inner pair often being larger than the outer pair, and the ventro-apical tubercles are small and inconspicuous.

In *E. floralis* (fig. 3 *c*) the eight pairs of tubercles have approximately similar positions to those of *D. cilicrura*. The ventro-apical tubercles are larger than in *D. cilicrura* and are clearly visible between the inner apical tubercles. There is a tendency for the base of each inner apical tubercle to fuse with that of the adjoining outer apical tubercle and in some individuals the degree of fusion is such that the tubercles assume a bifid appearance.

In *E. brassicae* (fig. 3 *b*) the tubercle pattern shows some modification though the eight pairs are recognisable. In this species the base of each inner apical tubercle is fused with that of the adjoining ventro-apical tubercle to form the characteristic bifid tubercles. The evidence supporting this origin of the bifid tubercles was obtained by examining a large number of larvae. They showed marked individual differences in the shape of the bifid tubercles and their angle with the body. In some the fusion was incomplete in the first instar, and in others asymmetrical growth resulted in a bifid tubercle on one side of the median line and two distinct tubercles in the relative positions of inner apical and ventro-apical tubercles on the other. Gemmill (1927) who studied *Leptohylemyia coarctata*, the wheat bulb fly, which has the same tubercle pattern as *E. brassicae*, stated that in larvae dissected from eggs, " The two double spines [bifid tubercles] appear each as a pair of little separate knobs which afterwards become carried out on a common base to form double spines. Not a few larvae were hatched out in the laboratory in this condition, and, indeed, it was not uncommonly found in larvae from earlier infected field plants ".

In *P. fugax* (fig. 3 *d*) the tubercle pattern shows other modifications. Six pairs of tubercles are similarly large and conical, and the dorsal and lateral pairs are situated near the rim of the dorsal oblique area and so form part of the conspicuous corona. The inner apical tubercles are much reduced and lie a little in front of the outer apical tubercles. The bases of the ventro-apical tubercles are fused and form a median bifid tubercle which appears to take the place of the inner apical tubercles on the apical ridge.

Puparia.

The puparia of the several species are similar in form. They are sub-elliptical with the sides smoothly rounded and they lack outgrowths associated with the development of adult metathoracic spiracles in certain related genera. Characters of the larval cuticle remain visible and the puparia can be distinguished by the pattern of the hardened protuberances which are the remains of the tubercles of the eighth abdominal segment.

Summary.

A study of the immature stages of the Anthomyiid flies, *Delia cilicrura*, *D. trichodactyla*, *Erioischia brassicae*, *E. floralis* and *Pegohylemyia fugax*, associated with injury to cruciferous crops, has shown that the several species can be distinguished. The egg stage can be identified by the sculpturing of the chorion, except in the case of the closely related species *E. brassicae* and *E. floralis* where the sculpturing is similar but there is a considerable difference in size.

The larvae can be distinguished by differences in the shape and character of the head and in its relation to the prothorax, and in the form of the mouth-parts in the three instars. The number of finger-like processes of the anterior spiracles and the number and arrangement of the tubercles of the eighth abdominal segment also contribute to the identification of the larvae.

Acknowledgements.

The writer acknowledges gratefully the help and advice given by Professor H. W. Miles who also assisted in preparing the illustrations for publication. These studies were begun while the author was in receipt of a grant from the Agricultural Research Council and have been continued at Wye College through the courtesy of the Principal, Observations on *H. floralis* were made possible by the kindness of Dr. G. D. Morison, Aberdeen University, who sent puparia which gave rise to flies that bred in captivity.

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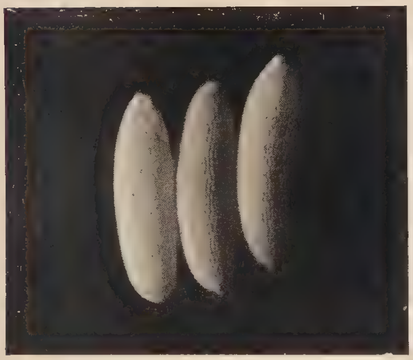

FIG. 1. Eggs of *D. cilicrura* (x 32).

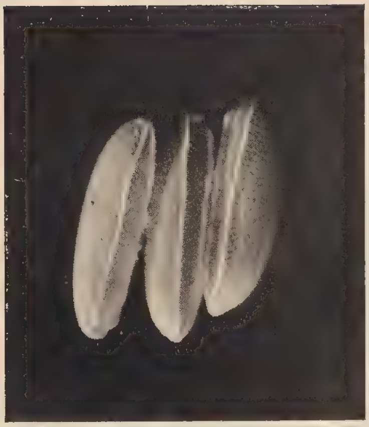

FIG. 2. Eggs of *P. fugax* (x 30).

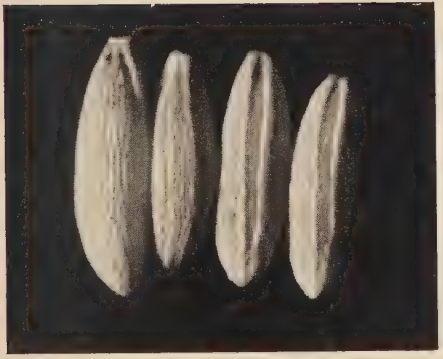

FIG. 3. Eggs of *E. brassicae* (x 37).

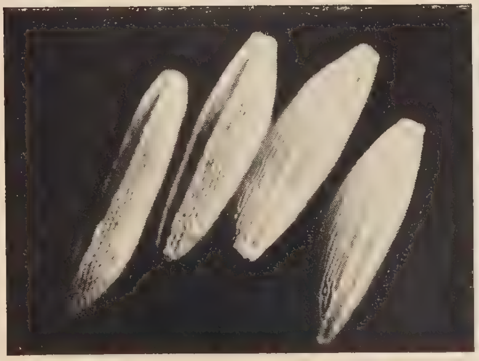

FIG. 4. Eggs of *E. floralis* (x 32).

SOME FACTORS AFFECTING THE AVAILABILITY OF CONTACT INSECTICIDES.

By F. Barlow and A. B. Hadaway.

Colonial Insecticide Research Unit, Porton.

The object of this paper is to point out that the physical state of an insecticide as it affects its availability is of great importance when comparisons are made between different contact insecticides on different surfaces. This is especially important when flying insects and relatively short contact periods are involved, as in such cases each insect must pick up and carry away a toxic dose.

It is convenient to divide the paper into three sections under the headings, Oil Solutions, Emulsions and Aqueous Suspensions, and to consider the physical state and availability of the deposits obtained when these three types of formulation are sprayed on to different materials.

Oil Solutions.

It would seem likely that because the outer layers of the insect epicuticle are essentially lipoid in nature and are easily wetted by oils, a contact insecticide would be more rapidly effective in an oil solution than as a dry deposit, provided that both are equally available to the insect. The following observations indicate that this is so.

When oil solutions of DDT are applied to a non-absorptive surface such as glass, the films or droplets are initially very toxic to mosquitos and tsetse flies. Contamination of the tarsi takes place and the insecticide penetrates the cuticle.

Evaporation of the solvent usually results, under normal laboratory conditions, in a mixture of crystals and supersaturated or supercooled droplets. The more volatile the solvent, the greater is the proportion of liquid droplets. These droplets eventually crystallise on exposure, or may be induced to crystallise by mechanical stimulation with brush or needle or by insects walking over the surface. Crystallisation takes place more rapidly from a continuous oil film than from droplets and gives a smaller proportion of supersaturated drops. It also takes place more rapidly from solutions of pure pp′ DDT than from solutions of crude commercial DDT. On glass, the sequence of events during evaporation is very haphazard and practically impossible to predict with certainty. The condition of the resulting deposit varies from one application to another. This has also been found by Vickers (1947) and Bruce (1949). However, when crystallisation has been completed, there is a marked reduction in toxicity. It is possible that many of the reported synergistic effects with DDT are due to inhibition of crystallisation from oil solutions by the various materials added.

A 5 per cent. solution of pp′ DDT in kerosene was sprayed on to glass plates at a dosage of 100 mg. DDT per sq. ft. Three hours later, tsetse flies, *Glossina palpalis* (R.-D.), were exposed individually to them for 15 seconds' contact, and 100 per cent. kills resulted. Crystallisation had taken place after 24 hours, and no kills of tsetse flies were then obtained after 15 seconds' contact with the dry deposit, which consisted of needle crystals lying flat on the surface. A similar solution of DDT in a mixture of 90 per cent. kerosene and 10 per cent. cotton-seed oil was sprayed on to glass plates at the same dosage at the same time. After 24 hours, the DDT had crystallised in the same form as from kerosene alone, but the crystals were coated with a tacky oil film, and 100 per cent. kills were obtained when tsetse flies were exposed for 15 seconds' contact with the deposit 3 and 24 hours after application.

A dosage of 25 mg. DDT per sq. ft. was applied to glass plates by spreading a 5 per cent. solution and by spraying the required volume in a tower and mosquitos, *Aëdes aegypti* (L.), were exposed to the deposits at various times after application. The resulting kills are given in Table I.

TABLE I.

Kills of mosquitos (*A. aegypti*) exposed for short contact periods to deposits from oil solutions on glass plates.

Solvent	Method of application	Age of deposit	Description of deposit	Mean percentage kill in 24 hours after exposure of (in minutes) :—						
				0·5	1	2	4	8	16	32
Kerosene ...	Spreading	3 hours	Continuous oil film ...	100						
		2 days ...	Dry, crystalline			0	0	0	0	
		7 days ...	—							
Kerosene ...	Spraying ...	3 hours	Discrete oil drops ...	100						
		2 days ...	Mostly drops, few crystals	55	93					
		7 days ...	Mostly crystals, few drops				0	18	30	83
9K : 1C.S.O.*	Spraying ...	3 hours	Oil drops...	100						
		2 days ...	Crystalline, with tacky film	98						
		7 days ...	Crystalline, less tacky ...	0	25	60	95			
1K : 1C.S.O....	Spraying ...	3 hours	Oil drops, no crystals ...	100						
		2 days ...	Oil drops, no crystals ...	100						
		7 days ...	Oil drops, no crystals ...	100						

*K=kerosene. C.S.O.=cotton-seed oil.

Similarly, a commercial oil-bound DDT suspension was found to be more effective than the most effective size (10–20 μ) of DDT crystals on a non-absorptive surface. This was shown to be due to the presence of the oil solution of DDT, which was non-effective on an absorptive plaster surface. Results of this test are given in Table II.

TABLE II.

Kills of mosquitos (*A. aegypti*) exposed for short contact periods to deposits on glass plates.

Formulation	Dosage	Mean percentage kill in 24 hours after exposure of (in minutes) :—							
		0·25	0·5	1	2	4	8	16	32
10–20 μ DDT crystals	50 mg. DDT/sq. ft.			8	38	83	100		
10–20 μ DDT crystals + spindle oil saturated with DDT*	50 mg. DDT/sq. ft. +35 mg. oil/sq. ft.	50	88	100					
Spindle oil saturated with DDT ...	35 mg. oil/sq. ft.	88	100	100					
40–80 μ DDT crystals	50 mg. DDT/sq. ft.						0	8	30
40–80 μ DDT crystals + spindle oil saturated with DDT	50 mg. DDT/sq. ft. +35 mg. oil/sq. ft.	40	78	100					
Spindle oil saturated with DDT ...	35 mg. oil/sq. ft.	83	100	100					

*35 mg. spindle oil saturated with DDT contained 1·9 mg. DDT.

Other authors have observed this reduction in toxicity following crystallisation. For instance, Kruse (1948) exposed cockroaches, *Blattella germanica* (L.), for a 30-

minute contact period to glass plates treated with DDT in various solvents. Crystallisation during the 24 hours following application resulted in a considerable reduction in the toxicity of deposits. Elmendorf & others (1946) painted screens of copper gauze with solutions of DDT in various solvents. With the most volatile solvents, the DDT was left in a dry crystalline state and soon lost its capacity to kill mosquitos by four momentary contacts. These workers and others have found that the ineffective dry deposits could be reactivated by spraying with the solvent alone. Elmendorf & others also showed that if a diesel oil was added to the solvent the effectiveness persisted for a longer time. This is confirmed by the experiments with cotton-seed oil described above.

Thus it may be concluded that the most potent form of DDT deposit is as an oil film and if this could be maintained on the surface of the treated material the best control of insect pests would be obtained. It has been seen that the inclusion of 10 per cent. of a vegetable oil in a kerosene solution does not prevent crystallisation but increases the effectiveness of the deposit by maintaining an oil film on the crystals. The oil used was semi-drying and the inclusion of a non-drying, non-volatile oil would make the film even more persistent. Wigglesworth (1942) studied the effects of the type of oil used upon the rate of penetration of pyrethrum through the cuticle of nymphs and adults of *Rhodnius prolixus* Stål and showed that pyrethrum enters more rapidly when in light than in heavy petroleum oils, and very slowly when vegetable oils are used.

S. Davidovici, Z. Levinson & S. Reuter (unpublished, 1950) have also noted that complete crystallisation of DDT from the solvent seems to coincide with a considerable reduction in toxicity, and that the addition to the solvent of a substance that prevents the rapid crystallisation of the DDT in the residue would increase the duration of the insecticidal effect. The most promising results were with DDT solutions and emulsions to which Lanoline and parent substances had been added. Five per cent. DDT and 5 per cent. Lanoline in kerosene gave considerable reductions in houseflies even where the flies were known to be DDT-resistant. The effect was of only three weeks duration, however, and it was noticed that numerous crystals of DDT appeared on the sprayed surfaces three weeks after spraying.

One disadvantage of oil solutions used outdoors is shown by Lindquist & others (1946), who found that DDT is more readily decomposed by sunlight in solution than as a solid deposit. Loss of effectiveness was greater after the use of auxiliary solvents with high boiling points or ranges.

It is interesting to note that Musgrave (1948) recorded that of four samples (I–IV) of gamma isomer of benzene hexachloride, one (I) was more insecticidal than the other three to adults of *Dermestes maculatus* Deg., when the samples were tested as films formed on glass plates from chloroform solutions. A microscopical examination of the chloroform films showed that those prepared from sample I were different from the others. After a few hours, films of II, III and IV had crystallised, whereas those of I, prepared at the same time and under the same conditions, had not ; they were in the form of discrete globules. When residual films of the insecticides in a light, refined paraffin spray oil were prepared and tested, samples II and III were at least as toxic as I. Examination of residual films, resulting from light paraffin solutions, in which crystallisation was considerably retarded in every case, showed that films of samples I and IV were the most retarded. No full explanation of these observations was given, but it was suggested that the unexpectedly high toxicity of sample I was associated with traces of chloroform retained by the film. A probable explanation is that, as with DDT, an oil film of the gamma isomer of benzene hexachloride is more rapidly effective than a crystalline deposit. Another similarity between gamma isomer of benzene hexachloride and DDT is that crystallisation of the technical samples I and IV was retarded more than that of the refined samples II and III.

This work with non-absorptive surfaces such as glass, wire, etc., shows that a great loss of effectiveness occurs when insecticides crystallise from solution. Parkin and Green (1947), however, concluded that the reverse is true on wall-board. They sprayed squares of wall-board, an absorptive material made from compressed paper, with solutions of DDT in kerosene and exposed houseflies to the treated surfaces four days and four weeks later. It was shown that, with certain combinations of concentration and deposit, the residual film left by the spray increased markedly in toxicity to flies between the four-day and four-week exposures. In the interim between the two exposures, those boards on which the film had become more effective were observed to have developed a lighter-coloured area corresponding with the area of the petri dish under which the flies had been confined. This area was thickly carpeted with crystals, while relatively few crystals occurred on the remainder of the surface. Only single crystals very sparsely distributed or small bunches of crystals could be seen on treated wall-board before the first exposure to flies, and it was therefore assumed that the DDT was present almost entirely in the form of a supersaturated deposit and that in this form it was markedly less toxic than when crystalline.

Tests with mosquitos (*A. aegypti*) on compressed fibreboard, a material similar to that used by Parkin and Green, sprayed with kerosene solutions of DDT confirmed these results. It appears, however, that the increase in toxicity following the first exposure of mosquitos is due to an increase in the availability of the insecticide and does not mean that crystalline DDT is more toxic than a supersaturated solution. Initially the oil is absorbed into the fibreboard and is not readily available for contact with insects. Movement of insects on the surface induces crystallisation and needle crystals grow at right angles to the fibres. A dense mass of crystals appears on the surface and they are readily available to, and detachable by, insects walking on it.

This marked increase in toxicity of the deposit on wall-board is in contrast to the results obtained on glass. As mentioned previously, a 5 per cent. solution of DDT in kerosene on glass usually gives crystals which lie in the plane of the surface and are presumably not so easily detached.

Block (1948) described a similar " blooming " of DDT crystals from surface coatings. The toxicity to houseflies of surface coatings containing DDT tends to increase with time, and the formation of DDT crystals on the surface upon ageing was demonstrated in several types of coating. The DDT crystals could be seen clearly after mechanical stimulation as a white dust, and even after several months and repeated wiping, the crystals reappeared at the surface within a few days. The continued deposition of crystals at the surface of the coating is attributed to slow precipitation from a supersaturated solution of the insecticide in the paint vehicle. It can be shown that if the composition of the resin mixture is such that crystallisation occurs spontaneously throughout the film, then " blooming " cannot occur subsequently and the insecticide is rendered ineffective, as there is now a layer of plastic between the insecticide and the insect. The percentage of plastic in such a crystallised film can be reduced to a very low value and still prevent effective contact. Thus one part of chlorinated rubber to 200 parts of DDT decreased the efficiency against *Tribolium* very markedly.

Further investigations were made to determine to what extent this phenomenon occurs with other surfaces and insecticides. The results were only assessed visually and no biological tests were made. When a 5 per cent. kerosene solution of DDT was sprayed at about 100 mg. DDT per sq. ft. on fibreboard, spontaneous crystallisation occurred slowly over several days and was very different in appearance from the crop of crystals induced by insects or by brushing. The spontaneously grown crystals were long, from about 50 to 300 microns, rather stout and arranged in isolated clusters. Crystals induced by mechanical means, however, appeared as a dense uniform mat of thin needles about 50 to 150 microns long which completely obscured the surface of the board and which obviously projected for a considerable distance above it. The maximum growth of induced crystals was obtained by stimulation a few hours after the application of the kerosene solution. Deferment of the application of the stimulus for longer and longer periods resulted in smaller and smaller crops of induced crystals until, after four or five days, when presumably all the DDT has spontaneously crystallised, mechanical stimulation had no effect. Before this time was reached, the bloom could be removed by wiping and the induced crystallisation would occur again, although not usually to the same extent as in the first crop.

A 5 per cent. solution of DDT in kerosene was applied as single drops to the surface of various materials which were examined after mechanical stimulation by brushing. Induced crystallisation occurred to a markedly greater extent on fibreboard and filter paper than on any of the other materials, although cardboard, Essex board, cork and a velvet did respond quite noticeably. The induced crystals on these four materials were, however, very much smaller than those on fibreboard and were about 1 to 5 microns long. The time after application during which crystallisation could be induced was shorter with filter paper than with fibreboard. There was no difference between spontaneous and induced crystallisation on poplin, a short-pile carpet, unpainted wood and a porcelain tile. No detectable crystallisation was observed on the surface of mud blocks. DDT always crystallised from the fibrous materials in the form of needles projecting away from the fibres. This is in contrast to the usual recumbent crystallisation of DDT from kerosene on glass.

Certain other insecticides were applied in the same way, as 5 per cent. solutions in kerosene on fibreboard. None of these showed the same striking bloom of induced crystallisation as DDT. DDD and dieldrin gave a slight bloom on brushing, gamma-BHC gave isolated large hexagonal plates, and the ethylene derivative of pp′ DDT, methoxychlor, aldrin and toxaphene gave no crystals.

These observations show that it would be wrong to compare the potency of insecticides of different physical properties by application in volatile oil solutions to such materials as fibreboard and filter paper. The movement of insects walking over these surfaces treated with DDT would induce crystallisation and increase the availability of the insecticides, whereas some other substances would be denied this advantage. Again, the availability and consequent insecticidal effect of needle crystals of DDT projecting from the surface of fibreboard must be very different from those of, for example, isolated large hexagonal plates of gamma-BHC.

Various concentrations of pp′ DDT in 38 solvents differing in chemical nature and boiling point were applied as single drops to fibreboard. The results are not given in detail because, as would be expected, the behaviour shown depended upon the physical properties of the solvent and not on its constitution. The two important factors were the volatility of the solvent and its ability to dissolve DDT. The best examples of induced crystallisation were obtained with intermediate concentrations such as 5–10 per cent. and solvents of medium boiling points (about 120–200°C.). Lower-boiling solvents, although giving a marked crop of crystals a short time after application, showed rapid and extensive spontaneous crystallisation. Solvents boiling considerably above 200–250°C., on the other hand, only gave slow spontaneous crystallisation and brushing had no effect. High concentrations of about 20–40 per cent. in good solvents gave residues which crystallised only slightly or not at all. Low concentrations in high-boiling solvents also gave little or no crystallisation even after several weeks. Induced crystals from the different solvents did not markedly increase in size as the boiling point increased, but the spontaneous crystals were larger as they had longer time to grow.

It is assumed for these generalisations that the solvent easily wetted the surface. Alcohols did not do so and low-boiling solvents evaporated before soaking into the board and consequently left a solid incrustation outside.

The application of oil solutions, *e.g.*, kerosene solutions, to absorptive materials such as mud and plaster results in the absorption of the insecticide with the solvent. No detectable crystallisation was observed on the surface of mud blocks sprayed with 5 per cent. DDT in kerosene solution. Surface deposits on mud blocks sprayed with DDT solutions have been determined by Hadaway and Barlow (1949), and it was shown that only a small proportion of the total insecticide is available on the surface for contact with insects alighting on or walking over it.

Thus it may be concluded that insecticides such as DDT are more effective if they are dissolved in an oil film which is available to the insect, but that when the solvent has evaporated the efficiency of the residue will be governed by its physical condition. This in turn varies with solvent, concentration and type of surface, assuming that climatic conditions are constant.

Emulsions.

The observations made concerning oil solutions also apply to a large extent to emulsions which, on many surfaces, behave as oil solutions with probably some additional complications due to the presence of sticky and hygroscopic materials such as emulsifiers and stabilisers which increase adherence.

Bruce (1949) has described the deposits on glass and wood from emulsions of DDT in different solvents. On glass and less noticeably on wood, the size of the DDT crystals depended on the speed of crystallisation which, in turn, depended on the physical properties of the solvent ; rapid crystallisation produced crystals of small size. Toxicity tests with houseflies showed that a loss of toxicity occurred on glass as the emulsion dried. On wood, " blooming out " or crystallisation of DDT on the surface resulted in an increase in toxicity similar to that occurring with a kerosene solution on wall-board. Flies had to be on the surface not later than the second day to obtain a secondary bloom with xylene as solvent. On certain pieces of wood, when a bloom occurred on the soft part of the wood, it did not occur on the annual rings.

Aqueous Suspensions.

When aqueous suspensions of insecticides are sprayed on to porous materials such as mud and plaster, the wetting-agent solution penetrates into the material and leaves the solid particles on the surface. Surface deposits on mud blocks are very much greater, therefore, from aqueous suspensions of wettable powders than from kerosene solutions, and differences in availability of the insecticide to insects making contact with the surface are shown by differences in kills (Hadaway & Barlow, 1949). Similarly, plaster blocks sprayed with an aqueous suspension of a DDT wettable powder at a dosage of 100 mg. DDT per sq. ft. are very much more toxic to mosquitos than are those sprayed at the same dosage with a 5 per cent. solution of DDT in kerosene. This is shown by the results given in Table III.

TABLE III.

Kills of mosquitos (*A. aegypti*) exposed for short contact periods to plaster blocks sprayed with 100 mg. DDT per sq. ft.

Formulation	Mean percentage kill in 24 hours after exposure of				
	1 min.	2 mins.	4 mins.	8 mins.	16 mins.
Suspension of DDT wettable powder	5	28	48	88	
DDT-kerosene solution		0	0	0	0

Further studies by Hadaway and Barlow (1951) show that the effectiveness of surface deposits from aqueous suspensions of insecticides against mosquitos exposed for short contact periods is related to the size and shape of the insecticidal particles. For instance, with DDT on mud blocks there is an inverse relation between effectiveness and the size of the ground DDT particles. Particles of ground DDT less than 20 microns in diameter were the most effective against mosquitos. Differences in effectiveness of particles in various size ranges are attributed to differences in the amount of insecticide picked up and retained by the insect.

The presence of an inert diluent may reduce the availability of the insecticide particles in deposits from aqueous suspensions of wettable powders. This may be due both to a masking effect as a result of coverage of a proportion of the insecticide particles by the diluent and to adherence of the inert particles as well as the insecticide particles to insects. The probability of a lethal dose of insecticide particles adhering to an insect becomes less as the proportion of inert particles increases. McCauley, Fay and Simmons (1948) found that a DDT suspension from a 90 per cent. water-wettable powder was more effective than a DDT suspension from a 50 per cent. water-wettable powder against *Anopheles quadrimaculatus* Say in rooms treated at a dosage of 200 mg. DDT per sq. ft. Lord (1950) used dusts containing ground insecticides and a carrier (talc) against *Tribolium castaneum* (Hbst.) and showed that the effects of changes of concentration of DNOC, gamma-BHC and DDT on the toxicity of the insecticide were much greater than those due to corresponding changes in the amount of dust applied. The higher concentrations were more effective. Hadaway and Barlow (1951) found that the effectiveness of a given dosage of 20–40 micron DDT crystals on plaster blocks against *Aëdes aegypti* decreased as the amount of inert diluent (speswhite kaolin) increased.

Adherence of insecticide particles to the surface of the material sprayed is of importance in determining the availability of deposits from aqueous suspensions. This may be influenced considerably by the wetting agents used to disperse suspensions. The wetting-agent solution remains on the surface of non-porous materials with the insecticide particles and, on drying, causes them to adhere strongly to the surface. The crystals are therefore less available for pick-up and are less effective on glass than on plaster. For instance, mosquitos (*A. aegypti*) in contact with deposits of 10–20 micron DDT crystals at a dosage of 25 mg. per sq. ft. picked up 0·48 microgramme DDT per insect in 0·5 minutes on plaster but only 0·1 microgramme in 8 minutes on glass. Mean percentage kills in 24 hours after contact periods of 0·5 minutes on plaster and 8 minutes on glass were 62 and 12, respectively.

The importance of the presence of the wetting-agent solids in affecting the availability of particles is emphasised by results obtained with aqueous suspensions of 10–20 micron DDT crystals on two samples of compressed wallboard. The two samples looked alike but one (A) wetted fairly easily and the other (B) did so only with difficulty. On sample A, deposits were more readily available for pick-up and more effective against mosquitos after short contact times than on sample B (Barlow & Hadaway, 1952).

There is evidence that penetration of the wetting-agent solution into a porous material is not complete and that even the small amount of wetting agent remaining with the particles on the surface may be of importance on some materials. For instance, deposits from a dry mixture of DDT particles and an inert diluent dusted on to the surface of plaster blocks are more available and more effective than those from aqueous suspensions of DDT crystals or of a commercial wettable powder. Furthermore, whereas the availability of deposits of dry dusts on plaster is not affected by the relative humidity of the atmosphere, that of deposits from aqueous suspensions is (see Table IV).

Plaster blocks were sprayed with aqueous suspensions of 10–20 micron DDT crystals and kept for 24 hours in desiccators at different humidities. Kills of mosquitos exposed for short contact times on blocks kept at relative humidities below 50 per cent. were very much higher than those on blocks at high humidities. When the blocks kept at low humidity were stored at a high humidity for a further 24 hours, and *vice versa*, the kills were also reversed, and higher kills were always obtained on blocks kept at low humidities. The difference in kills was shown to be due to a difference in availability by chemical determinations of the weights of DDT picked up. The mean weight of DDT picked up by 40 mosquitos exposed for a contact time of 2 minutes to the blocks kept over sulphuric acid was 1·1 microgramme per mosquito in one test and the same in a duplicate test. Corresponding pick-ups from the blocks kept over distilled water were 0·2 and 0·1 microgramme.

TABLE IV.

Kills of mosquitos exposed to deposits of DDT formulations at a dosage of 25 mg. DDT per sq. ft. on plaster blocks kept at different humidities.

Formulation	Relative humidity	Mean percentage kill in 24 hours after exposure of				
		0·25 min.	0·5 min.	1 min.	2 mins.	4 mins.
Dry dust	100	70	100			
	0	80	100			
Commercial wettable powder ...	100			0	0	10
	0			15	65	100
Aqueous suspension of 10–20 μ crystals	100				5	
	75				50	
	0				98	

A difference in availability of 0–10 micron crystals occurs on mud and plaster, both porous materials. On plaster blocks, 0–10 micron DDT crystals are less effective than 10–20 micron particles against mosquitos exposed for the same short contact periods. The reverse is true, however, when aqueous suspensions of crystals in these two size ranges are applied to mud blocks. The mean weight of DDT picked up by 80 mosquitos in 0·5 minutes from deposits of 25 mg. 0–10 micron crystals per sq. ft. on mud blocks was 0·21 microgramme per mosquito ; the mean percentage kill of mosquitos exposed for the same contact time was 98 per cent. These figures correspond with those obtained after a contact period of 4 minutes on plaster blocks. Obviously the 0–10 micron particles are more readily available to mosquitos on mud than on plaster. Adhesion of the small particles to the substrate may be greater on plaster than on mud.

" Stickers " such as glue, gelatine, casein, and flour are often added to aqueous suspensions to increase persistence of deposits which have to withstand the weathering action of rain (*e.g.*, deposits on foliage). As the particles are more firmly attached to the surface they are less easily removed by insects. This is not important when the deposits are stomach poisons directed against leaf-eating insects, but it is important when the insecticide is directed against flying insects (*e.g.*, tsetse flies) which remain in contact with deposits for relatively short periods. A balance between resistance to weathering and availability to insects must be obtained by careful selection of the " sticker " and the concentration at which it is used.

Rubber latex in different concentrations was added as a " sticker " to aqueous suspensions of a commercial 50 per cent. DDT wettable powder, and the suspensions were sprayed on to glass plates at a dosage of 50 mg. DDT per sq. ft. Mosquitos were exposed to the plates for 32 minutes' contact, and the resulting kills, shown in Table V, decreased as the proportion of rubber latex increased.

TABLE V.

Kills of mosquitos (*A. aegypti*) after exposure to deposits from wettable powders containing rubber latex.

	Percentage of rubber latex on weight of DDT	Mean percentage kill in 24 hours after exposure of 32 minutes
Series 1 ...	0	94
	1	69
	5	36
	10	24
Series 2 ...	0	83
	0·1	58
	0·3	68
	1	55
	5	33

Conclusions.

When comparing the potency of several insecticides in the laboratory, due attention is usually given to standardisation of the method of testing and of environmental conditions. It is equally important that every substance should be in the same physical condition and be equally available to the insects.

For the control of insect pests with contact insecticides in the field it is essential to determine which formulation will give the optimum effect on the material to be treated.

Summary.

The physical state of deposits from various formulations of insecticides applied to different materials is considered in relation to the availability of the insecticide to insects making contact with the surface of the treated material.

Applications of oil solutions of insecticides to absorptive material result in absorption of the solution, and the insecticide is thereby rendered ineffective. On a non-absorptive surface, oil solutions are the most efficient formulations, but only so long as the deposit remains wholly or partly liquid ; if evaporation of the solvent gives a dry crystalline residue, this is much less efficient than the original solution.

On some fibrous absorptive surfaces, a solution of DDT in oil remains in a supersaturated condition in and around the fibres. If crystallisation is stimulated by mechanical means, the resulting crystals project from the treated surface and it is suggested that, in these circumstances, crystals are more readily available to insects than the oil solution from which they were derived.

DDT on compressed wall board shows the induced crystallisation to a greater degree than other insecticides. It is concluded, therefore, that wall board and similar surfaces should not be used in comparing the potencies of chlorinated-hydrocarbon insecticides applied as oil solutions, as DDT would be more available than others. Some factors that affect the degree of induced crystallisation are mentioned.

Many of the observations made in this paper on the availability of oil solutions can be expected to apply also to emulsions.

Insecticides are more readily available when they are applied as solid suspensions to absorptive materials. Some of the more important factors that influence availability of particles are their size, the percentage of inert diluent present and their adherence to the sprayed surface. Some rather unexpected variations in adherence to surfaces are described, and supporting evidence is given from chemical determinations of the amount of insecticide removed by the insect.

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CHANGES IN THE FAT AND PROTEIN CONTENT OF THE AFRICAN MIGRATORY LOCUST, *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. & F.).

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It has long been realised that reserve substances must play an important rôle in the activities of locusts, but little experimental work has been done along this line until recently. Matthée (1945) has reported a higher fat content in phase *gregaria* than in phase *solitaria* of the fifth instar hoppers of *Locusta migratoria migratorioides* (R. & F.) and *Locustana pardalina* (Wlk.). Phipps (1950) determined the percentage of fat of the adult females of various ages of *Locusta migratoria migratorioides*. He also showed by dissection the changes in size of the fat body during development. Weis-Fogh (1950) flew *Schistocerca gregaria* (Forsk.) in a " roundabout ", and showed that fat is the main source of energy during flight. Papers concerning fat and protein content of some locusts and grasshoppers published up to the end of 1946 were reviewed by Uvarov (1948).

The object of the present study was to investigate the building up and the subsequent consumption of fat and protein reserves during the adult life of *Locusta migratoria migratorioides* under laboratory conditions. Special interest has been focused on whether the fecundity and maturation differences between the two phases as observed by Norris (1950) can be related to those reserves.

Materials and Methods.

All the locusts used, which were reared under standard conditions, were kindly supplied by the Anti-Locust Research Centre, London. They were mostly killed at various periods during adult life as required and sent as dried material. Those that were used in the observations on oviposition and feeding were, however, brought alive as they approached the desired stages of development and kept in the laboratory at Cambridge. The technique employed was essentially that described in the circular " Instructions for rearing and for breeding the African Migratory Locust " distributed by the Anti-Locust Research Centre (1948).

The fat was analysed by the Soxhlet extraction method and Kjeldahl's procedure was followed for nitrogen determination. The non-protein nitrogen was deducted from the total nitrogen and protein was calculated by multiplying this resulting nitrogen value by the protein conversion factor. Whenever possible not less than six locusts were analysed separately in each treatment. Preliminary experiments had shown that locusts of different developmental stages differ tremendously in the amount of undigested food in the gut. This could vary from 0 per cent. to 15 per cent. of the total dry weight. To obtain accurate results, it was found necessary to remove the gut contents before analysis. All values of fat and protein were, therefore, calculated on dry body weight after removal of the gut contents.

In order to show the changes in fat and protein contents due to egg-laying, some of the locusts and egg-pods were analysed immediately after oviposition. The composition of the same locusts before egg-laying could therefore be calculated by combining the values.

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As the process of build-up is intimately connected with the food consumption of an insect, it was thought helpful to make a quantitative study of the amount of feeding by the locusts. An indirect method was finally adopted, namely the daily weighing of the dried faeces, produced by the locusts, as a rough index of the quantity of food consumed. The method could not be exact, for the amount of faeces produced must alter when the efficiency of food assimilation or the amount of nitrogen compounds excreted alter, but the results corresponded with observations on the amounts eaten.

Feeding and Body Weight.

The general picture of the building up of reserves in the locust will be more easily appreciated if the data on feeding (fig. 1) and the changes in body weight (Table I) are presented first.

Adult locusts of phase *gregaria* reared in the laboratory begin to feed about 12 hours after the final ecdysis. The female eats voraciously for a period of ten days or a fortnight. During this period, as shown in Table I, the insect roughly doubles its dry weight in the first week and re-doubles it in the second. The wet weight does not increase so much, for the amount of water in the body decreases (Webley, 1951). Then follows a period of less active feeding until after the deposition of the first egg-pod ; little change in body weight is taking place within this period ; but as will be shown later, this does not mean that the insect is physiologically inactive.

Immediately after egg-laying the insect, having lost one-fourth of its total body weight, again starts to eat voraciously. This feeding continues for a day or two, then drops and reaches its minimum when the next egg-pod is about to be laid. The same cycle is repeated whenever a new egg-pod is deposited. By replacing lost weight quickly after each laying, the insect is able to maintain a fairly constant body weight. Locusts which have laid six egg-pods have the same body weight as those which have laid only once.

A complete curve of feeding activity in the female (of both phases), as seen in fig. 1, shows a rise that is correlated with the initial build-up of reserves, followed by a number of well-marked minor peaks each preceding the deposition of an egg-pod.

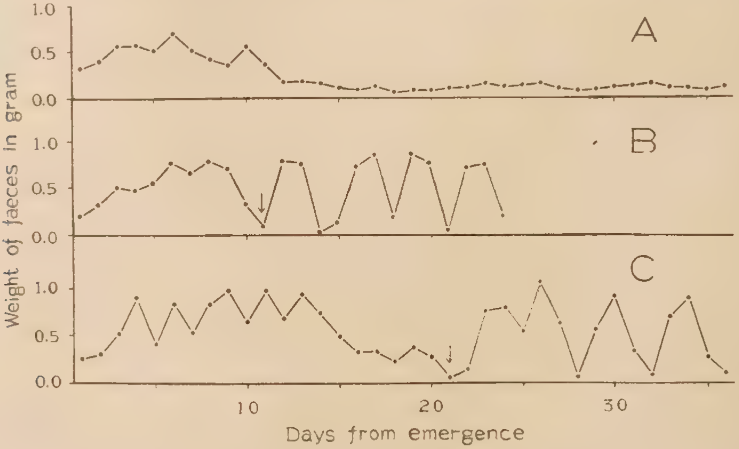

Fig. 1.—Feeding activity curves of adult locusts. A, *gregaria* male ; b, *solitaria* female ; C, *gregaria* female. Ordinates : dry weight of faeces produced each day in grammes. Abscissae : number of days from emergence. The arrows show the times at which the first egg-pods were laid. Only four each of the subsequent build-up cycles are shown in B and C.

TABLE I.

Fat and protein content at various stages of development of the adult locust.

Phase and sex	Age	Fat		Protein				Dry body wt. mg. per locust
		% to dry wt.	mg. per locust	% to dry wt.	% to fat-free dry wt.		mg. per locust	
Gregaria female ...	1 day	13·9± 1·7	40 ± 7	55·0	62·0		169±16	284
	1 week	25·1± 3·7	152 ±27	45·4	59·9	61·2±2·4	237±39	523
	2 weeks	30·1± 5·4	317 ±56	40·3	61·4		414±35	1,052
	Before 1st laying ...	15·5± 1·5	165 ±27	56·2	66·5		607 ±62	1,063
	After 1st laying... ...	14·9± 2·0	119 ±26	56·5	66·7		462±57	798
	5 weeks	17·8± 9·5	143 ±87	—	—		—	802
	7 weeks	12·1± 4·9	93±48	—	—	66·5±1·6	—	771
	After 6th laying... ...	8·5± 1·9	68 ±13	60·5	66·3		484±57	802
	At time of death ...	7·2± 1·7	42 ±13	—	—		—	—
Solitaria female ...	1 day	5·3± 0·3	18± 2	57·4	62·5	62·1±2·9	197 ± 38	346
	1 week	13·5 ± 2·4	99±34	52·9	61·3		376± 42	710
	Before 1st laying ...	15·0± 6·8	178±99	55·0	65·3		667 ± 96	1,212
	After 1st laying... ...	14·4± 8·0	136±95	54·6	64·4	65·0±1·9	528±128	968
	After 6th laying... ...	10·8± 5·4	103 ±52	58·1	65·3		552± 68	956
Gregaria male ...	1 day	11·8± 0·2	28± 4	—	—		—	233
	1 week	22·9± 4·8	90±27	—	—		—	392
	2 weeks	29·9 ± 5·6	169±66	—	—		—	565
	5 weeks	23·3±12·2	123±87	—	—		—	526
	7 weeks	21·6± 6·5	110±49	—	—		—	508
	At time of death ...	5·4± 2·0	20± 9	—	—		—	—
Solitaria male ...	1 day	7·3± 0·8	15 ± 3	—	—		—	202
	1 week	10·9± 2·1	38± 9	—	—		—	353
	2 weeks	19·4± 2·2	96±15	—	—		—	493
	5 weeks	23·4±12·2	117±77	—	—		—	500
	7 weeks	10·6± 4·7	44 ±15	—	—		—	—

In nearly all treatments not less than six locusts analysed.

Adult locusts, one to seven days old, of which the wings were marked by coloured cellulose tapes, were kept under observation in a cage. A total of 16 observations on feeding were made. It was shown that the locust discharges approximately three faecal pellets during each feeding period irrespective of the frequency with which it eats or the amount of grass it consumes. From the number of faecal pellets produced it was thus calculated that the locust feeds 40 times within 24 hours at the height of its feeding activity. A single meal takes 4 to 25 minutes and one-seventh to one-fifth of the life of the locust is spent in eating. By the time the female lays its sixth egg-pod, the total amount of dried faeces produced during adult life amounts to 25 times its own dry body weight.

The feeding activity curve in the *solitaria* female, as measured by the weight of faeces produced each day, agrees with that of the *gregaria* female in its general shape. The only difference lies in its shorter build-up periods both before maturation and after each oviposition. The *solitaria* female also attains its maximum body weight faster than the *gregaria*. Though the *solitaria* eats as much food per day as the *gregaria*, the total amount of grass consumed, as estimated by the weight of faeces produced, by the former up to the sixth oviposition is about one-fifth less, in view of the fact that this stage is reached earlier in the case of *solitaria*.

The males of both phases have definitely different feeding activity curves from the females. The initial active feeding period, corresponding to that of the females, is followed by a steady period of reduced feeding with little fluctuation throughout adult life. The insect maintains a constant body weight after the initial build-up period.

Fat.

The results of fat determinations with their standard deviations are summarised in Table I.

(1) Females of phase *gregaria*.

As shown in Table I, the locust begins to build up fat soon after the final ecdysis. By the end of the second week the fat has increased to the maximum of 30 per cent. (317 mg.) of the dry weight. Then a rapid disappearance of fat takes place during the period of reduced feeding that follows. At the end of the third week, just before the deposition of the first egg-pod, the insect has used up about 50 per cent. (152 mg.) of the total fat reserve which now represents only 15·5 per cent. of the dry weight. The reduction in size of the fat body before oviposition, after it has reached its maximum development, has also been reported by Phipps (1950). He writes : " The fat body reaches its maximum development in early Stage III ; later it is much reduced and where the eggs are fully developed only a few shreds of it remain."

After the first egg-pod, which contains an average of 46 mg. of fat, is laid, the insect has a fat content of only 15 per cent. (119 mg.). Although the fat eliminated in the subsequent egg-pods must be derived, at least in great part, from fat built up each time after a new egg-pod is laid, the fat content of the locust decreases gradually towards the end of the oviposition period.

It has been suggested by Uvarov (1948) that in *Melanoplus differentialis* (Thos.) the expenditure of fat is connected with egg development. The data presented in Table I show that in *Locusta* only a minor part of the fat of the immature insect goes into the eggs and the greater part is utilised by the female herself.

During the early part of the oviposition period the insects seem to be capable of replacing lost fat as fast as they use it, so that the 5-week-old locusts, which have normally laid 3–4 egg-pods, have a fat content comparable to that of the animals which are about to lay their first egg-pods ($t=0{\cdot}58$, $P>0{\cdot}05$, difference not significant). But locusts which have laid six egg-pods, of which the total amount of fat is estimated to be 280 mg., have only 8·5 per cent. (68 mg.) of fat, indicating that in the later part of the oviposition period they have used more fat than they have built up. The locusts have a fat content of 7 per cent. (42 mg.) when they die.

(2) Females of phase *solitaria.*

The newly emerged and the one-week-old females of phase *solitaria* have significantly less fat than those of the corresponding stages of phase *gregaria* ($t=13{\cdot}17$, $P<0{\cdot}01$; $t=6{\cdot}95$, $P<0{\cdot}01$). By the time the first egg-pods are about to be laid, the fat content, unlike that of *gregaria,* exhibits a great variation in amount. As shown in Table II, it varies from 7·4 to 24·4 per cent. and is found to be directly correlated with the length of the period from emergence to the time the egg-pod is deposited. This fact shows that the maturation of the eggs is independent of the development of the fat body and that the accumulation of a great amount of fat is not essential to an early deposition of eggs.

TABLE II.

Correlation between fat content and length of pre-maturation period in female *solitaria.*

Pre-maturation period in days	Percentage of fat	
	Before egg-laying	After egg-laying
11	7·4	6·2
13	9·3	7·4
13	10·8	9·3
14	14·6	13·2
15	20·6	20·9
33	24·4	26·0

One insect of each age. Percentage of fat after egg-laying calculated as on p. 104.

The *solitaria* female, as a rule, has a shorter pre-maturation period. Occasionally, however, they may mature as slowly as the *gregaria.* It is very interesting to note that in one case a *solitaria* female, which had a comparatively long pre-maturation period of 22 days, still had a fat content of 18·8 per cent. (180·6 mg.) after the deposition of the sixth egg-pod. This shows that a solitary locust, which has developed its fat body fully before oviposition, may be able to leave a great part of its fat reserve intact even at the end of the oviposition period. As we have seen, the fat reserves in the *gregaria* female are always reduced to a very low level at this stage.

(3) Males of both phases.

The fat in the males is built up during the early part of adult life in much the same way as in the females ; but it is used up much more slowly. As far as the percentage is concerned the immature males have about the same amount of fat as the females of the same age.

The course of the fat metabolism in the locusts of both sexes of phases *gregaria* and *solitaria* have one thing in common. Fat is rapidly built up in the early part of adult life. After reaching a peak it gradually disappears. It is interesting to compare these results with those of Pfeiffer (1945) on *Melanoplus differentialis* in which the fatty acid content follows a similar curve.

Protein.

The results of protein analysis with their standard deviations are tabulated in Table I.

(1) Females of phase *gregaria*.

As the dry insect body is mainly composed of protein, it was to be expected that the building up of protein would closely follow the increase of body weight. The weight of protein has finally reached its maximum when the insect is about to lay its first egg-pod. While fat is rapidly breaking down during the third week, protein is still being actively synthesised. This compensation makes the change of body weight during this period insignificant.

The loss of protein at egg laying is considerable. It is about one-fourth, 144·4 mg. (Table III) of the total protein built up by the insect before oviposition (Table I). But owing to the fact that the lost material after each laying must be rapidly replaced, the protein content of the locust remains fairly constant.

The percentage of protein calculated on the basis of dry body weight tells very little, for it fluctuates with the changes in fat content. When it is calculated on the basis of the fat-free dry body weight, it does show that the mature locusts have significantly more protein than they had when they were young ($t=7{\cdot}0$, $P<0{\cdot}01$). This increase in protein content in the mature locust may be partly due to the thickening of the cuticle with the deposition of protein in the endocuticle. Millot and Fontaine (1938) have reported the gradual increase in chitin content with age in adult *Schistocerca gregaria*. Chauvin (1941) has shown the difference in thickness of the cuticle between the immature and the mature locust.

(2) Females of phase *solitaria*.

The building up and the elimination of protein in the *solitaria* female differs in no respect from that of the *gregaria*. Although the *solitaria* has more protein by weight, which is obviously due to its larger size, it has the same percentage of protein as the *gregaria*. At oviposition the protein eliminated in the egg-pod is 131·7 mg. (Table III), which is about one-fifth of the total protein (Table I). This lower proportion of protein discharged, in comparison with that of *gregaria*, is due to the higher body weight of the *solitaria* female as well as to the smaller amount of protein in the *solitaria* egg-pod (Table III).

Egg-Pods.

As will be seen in Table III, the egg-pods of *solitaria* have more eggs per pod than those of *gregaria*, an observation which agrees with that of Norris (1950). The eggs in a *solitaria* egg-pod are, however, smaller in size as shown by the dry weight per 100 eggs. This difference is highly significant ($t=3{\cdot}25$, $P<0{\cdot}01$). The *solitaria* egg-pods are also slightly lower in weight, but this can not be considered as statistically significant ($t=1{\cdot}26$, $P>0{\cdot}05$). The egg-pods produced by *gregaria* females isolated after the final ecdysis are intermediate between the *solitaria* and the *gregaria* both in the number of eggs per pod and in the size of the eggs.

It is clear that high fecundity, as expressed in the number of eggs, does not necessarily mean more egg material.

Discussion.

No definite relation has been found in the present study between fecundity, rate of maturation or oviposition, and fat and protein content.

The relation between the maturation of the eggs and the body weight of the locust has been noted by Phipps (1950). His results together with the observations made in this work seem to indicate that locusts will not begin to oviposit until they have attained their maximum body weight. Probably, other things being equal and favourable, locusts will normally mature in accordance with the speed with which they increase their body weight. The body weight is, of course, a net result of the amount of substances an insect is capable of building up, minus that which is used up in the performance of various activities by the insect. The writer is inclined to think that the earlier maturation of *solitaria* is due to its more rapid build-up in the body weight, which is made possible probably by the lower metabolic activity of the insect. The higher rate of oviposition in the *solitaria* is, no doubt, due to the same cause.

TABLE III.

Weight, fat and protein content of egg-pods.

Phase	No. eggs per pod†	Dry wt. per 100 eggs (mg.)†	Dry wt. per pod (mg.)†	Fat*		Protein*	
				Per cent.	Mg. per pod	Per cent.	Mg. per pod
Gregaria	62·5 ±8·6	403±13	265±40	17·4	46·3	54·3	144·4
Gregaria isolated ...	66·5±9·5	396±29	263 ±37	—	—	—	—
Solitaria	72·7±9·6	338±42	246 ±29	17·7	43·6	54·0	131·7

*6 locusts were used in the case of each phase.

†18 locusts were used in the case of each phase.

This same view may also help to explain Norris' results (1950) that the reproductive performance in the *solitaria* is much less susceptible to adverse environmental factors, such as inferior food and crowding during adult life, than in the *gregaria*.

The pre-maturation period in locusts may vary considerably between individuals, but once the first egg-pod is deposited the subsequent pods will follow at regular intervals—so regular that it almost deserves the word "rhythmical". There is evidence to show that substances built up in the oviposition period are mainly devoted to the production of eggs. It is probable, therefore, that any activity such as flight, which demands a great amount of reserve substance, could take place during the oviposition period only at the expense of the proper development of the eggs.

Summary.

The process of build-up of reserve substances in *Locusta migratoria migratorioides* (R. & F.) is very closely correlated with the feeding activity of the insect. Locusts attain their maximum body weight in the initial period before maturation. In the females there is one minor build-up period after each laying.

As measured by the weight of faeces produced, the *gregaria* female consumes more food than the *solitaria* during development. It also has a lower rate of increase in body weight, maturation and oviposition.

Locusts start to build up fat soon after the final ecdysis. The fat content reaches its maximum in the early part of adult life, and then begins to decline in both sexes of both phases.

By far the greater part of the fat reserve thus built up in the *gregaria* female is used up *before* oviposition, and only a small amount goes to the making of the first egg-pod. The fat of the subsequent egg-pods (of both phases) is derived from the fat built up each time after a new egg-pod is laid.

The *solitaria* females may mature their eggs at various stages in the development of the fat body. Those which have a longer pre-maturation period have a higher fat content.

Immature *gregaria* females have significantly more fat than those of *solitaria*, almost twice as much at the maximum, but this difference disappears completely before the first egg-pod is laid. It is suggested that this extra use of fat by *gregaria* is connected with a higher rate of metabolism than that in *solitaria*. Data from one specimen of *solitaria* suggests, further, that a lower rate of metabolism in this phase enables fat reserves to be kept at a higher level throughout the egg-laying period.

The protein content of a female locust reaches its height just before oviposition. The protein lost during each laying is rapidly replaced by feeding. There is no difference in the percentage of protein between the *gregaria* and *solitaria*, although the *solitaria* has more protein by weight due to its larger size.

A mature locust has a significantly higher percentage of protein per fat-free dry body weight than the immature. This is probably partly due to the deposition of more protein in the cuticle as it thickens.

The egg-pods produced by the *solitaria* female were found to contain more eggs of smaller size than those of the *gregaria*. The difference in weight between the egg-pods of the two phases is, however, not statistically significant. High fecundity does not mean more egg material.

No definite relation has been found between fecundity, rate of maturation or oviposition, and fat and protein content.

It is suggested that the earlier maturation of the *solitaria* is due to its more rapid build-up in body weight, which is made possible because the insect probably has a lower metabolic activity. The higher rate of oviposition in the *solitaria* is attributed to the same cause.

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ENTOMOLOGICAL PROBLEMS OF FOOD STORAGE IN NORTHERN NIGERIA.

By R. W. HOWE.

Pest Infestation Laboratory.

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During the period 1948 to 1950, a team of entomologists and chemists under the leadership of Mr. G. S. Cotterell was set up in Nigeria by the Colonial Office to investigate local problems associated with the storage of produce prior to export. A brief official report of the findings of the team is being published. This paper gives in greater detail an account of the purely entomological work of the team in Northern Nigeria, excluding that on control measures. The work was restricted mainly to the problems of groundnut storage, which alone is considered in this paper, with a little attention to the storage of guinea corn for local use.

Storage Conditions.

Groundnuts are grown for export over most of the northern provinces of Nigeria. The size of crop has increased over the last ten years with the increased world demand for oil seeds, but the facilities for carriage of the nuts to the ports have not improved so rapidly. At present, yearly crops in the region of 300,000 tons can be expected in Nigeria and some 40,000 tons from adjacent French territories pass through to Nigerian ports. Consequently, storage centres near the railway have been continuously occupied by stored groundnuts for some five years.

Prior to 1946, it was customary for the whole of the crop of any one season to be moved before the next harvest in October, but in that year 5,000 tons remained when the new crop season commenced. In succeeding years, the crop overlap increased so that storage for as long as 18 months occurred occasionally. As a result more nuts had to be stored than could be accommodated in the warehouses and the Nigerian authorities devised an excellent outdoor method of storage in pyramids. All the observations described here were made in the Kano township where at least half of the total crop is stored. Conditions are similar in most of the other 20 groundnut storage centres.

Handling before storage.

Groundnuts are harvested in October and sun-dried on the plant. The nuts are removed from the plant by beating with sticks and shelled by pounding the nuts in a vessel with a heavy pestle, and winnowing off the husk. This rough method of shelling pulverises and splits many nuts so that the crop as stored contains roughly equal proportions by weight of whole nuts, split nuts and fragments. Average proportions in samples taken in November and December 1949 were, whole nuts 39·8 per cent., splits 32·6 per cent., fragments 27·6 per cent. These samples contained more whole nuts than in previous seasons. The sun drying ensures that nuts are comparatively dry when brought to store. This is further ensured legally by imposing an official ban on the sale of nuts before a given date fixed according to the harvesting date and the last rains of the season. The average moisture content of nuts going into store in Kano in the 1949 season was 3·4 per cent.

When selling is permitted farmers take their nuts to official buying stations, of which there are over one hundred, and they are bought by an agent acting for a licensed buying firm. The nuts are weighed, spread out on a mud platform and examined for extraneous material. Nuts from many sources are mixed and are sacked daily into standard packs of 189 lb. gross weight. The sacked nuts are stacked into rectangular stows nearby in the open, usually on the bare earth and are carried to storage centres by motor lorry as convenient. The nuts rarely remain more than a fortnight in buying centres but may, in exceptional circumstances, stay for as long as three months. If such long storage is anticipated the ground beneath the stows is covered with groundnut shell to prevent damage by termites. At the storage centre also the nuts may be stacked into small temporary stows for many days before going into more permanent stacks. Often a considerable amount of damage to the sacks is caused by termites in this period.

The major part of the groundnut crop is sold for export but a certain amount is retained for seed and as a local foodstuff. It also seems probable that a small quantity of nuts remain stored for a whole year before being sold for export. This obviously can only be done by wealthy individuals and is presumably speculative, taking advantage of rising export and local market prices. That it does take place was revealed in 1948–49, when measurements of the free fatty acid content (F.F.A.) of nuts in certain stacks was found to be very high. In 1949–50, the average F.F.A. of broken nuts in samples arriving in Kano was 0·8 per cent. If old nuts (*i.e.*, 1948–49) had been included this figure would be higher, but local market prices in 1949 exceeded export prices for a time so that it would have been unprofitable to have retained nuts for export.

Description of warehouses and pyramids.

All storage sites are placed as near as possible to railway sidings although more distant sites have been used when absolutely necessary.

All the warehouses have cement floors and corrugated iron roofs. The walls are of many kinds, corrugated iron, brick, stone, concrete, or mud faced with cement. They are lime-washed before the warehouse is used for a new crop. Many stores have a central row of supporting pillars either brick or concrete. Beams and rafters are of wood or concrete. The capacity of the warehouses is generally about 600 tons. Most of them are detached buildings but a few are not. All have some form of ventilation, often consisting of a space under the eaves.

Open-air storage is on specially constructed plinths. The size of these depends on the space available but the original size was usually 50 feet square. Later a plinth 100 feet long and 50 feet wide was adopted. The plinth is built about one foot up from the ground, a brick boundary wall being built first. The central foundation is made of stones, large stones being topped by smaller stones, laterite and cinders and often covered by groundnut shell. Cinders and groundnut shell are alleged to keep out termites and appear to do so very efficiently. The edges of the plinth are faced with concrete or mud. The mud is weather-proofed with a glaze made of red clay, cow dung and " dawa-dawa " pod extract (*Parkia filicordis*).

Sacks of groundnuts are placed flat on the cinders or shell. A base 50 foot square will accommodate 480 sacks, 30 side by side along one side by 16 end to end along the other. Layers are generally put down with the long axes of sacks in alternate layers at right angles. The first eight or so layers all contain the same number of sacks giving the pyramid a vertical edge for the bottom six or seven feet. Thereafter each succeeding layer is normally decreased in length by one sack so that the total height of the pyramid is about 40 sacks, and the vertical height of the pyramid just over 30 feet.

The sacks are carried to the higher layers up a stairway of groundnut sacks which is finally removed. Such a pyramid contains about 9,000 sacks or approximately 750 tons.

Pyramids built on rectangular bases are similar but are built to a ridge about half the length of the plinth, instead of to a point. Such cottage type pyramids are built to hold approximately 600 or 1,500 tons.

Rains fall between April and October, 70 per cent. of the total amount falling in July and August. Heavy falls are recorded on about 25 days. Pyramids must be protected against these rains and are therefore covered with rick sheets early in April, the sheets being placed so that the upper ones overlap the lower. The sheets are fixed in place by a lattice of horizontal and vertical ropes, tied together where crossing, and weighted with stones. The bottoms of the sheets are weighted with baulks of timber, iron, stones, etc., since exceptionally strong gusts of wind are liable to move the sheets. When the sheets are in place, trenches one foot wide and one foot deep are dug around each pyramid to collect the water run-off.

Temperature and humidity.

In Kano the pyramids are exposed to direct sunlight for much of the day and although the east and west sides each have a shady period, both north and south faces are subject to continuous sunlight all day. No figures are available for the temperature of pyramid surfaces in the sun, but fig. 2 shows the maximum and minimum temperatures and humidities at the top of a stack in a warehouse only a foot below the iron roof. Since these temperatures are probably lower than outdoor sun temperatures it is evident that insects exposed to the sun must either move into the shade of the stack or else be killed. Many insects hiding between overlapping rick sheets are, in fact, killed.

Shade temperatures and relative humidities for the years 1943–47 inclusive, supplied by the Nigerian Meteorological Service, are graphed in figs. 1 and 4. The points plotted in fig. 1 are the monthly means of daily maximum temperatures and relative humidity at 12·00 hours and of daily minimum temperatures and relative humidity at 6.00 hours. The enclosed area represents the range of mean conditions experienced during the year. In fig. 4 the mean monthly relative humidities at 6.00 and 12.00 hours are plotted, and also the monthly means of readings taken every three hours. The absolute maximum relative humidity of the three-hourly readings reaches 100 per cent. in August and September but is only 45 per cent. in February. The minimum relative humidity recorded for August is 71 per cent. and for February 12 per cent.

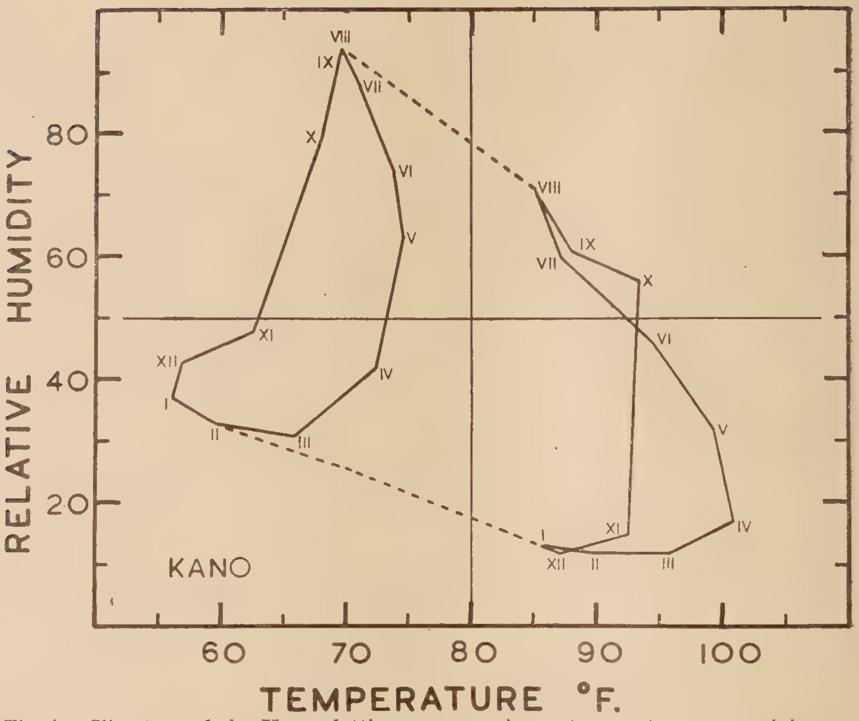

Fig. 1.—Climatograph for Kano plotting mean maximum temperature-mean minimum relative humidity at 12.00 hours and mean minimum temperature-mean maximum relative humidity at 6.00 hours for each month from ordinary meteorological records.

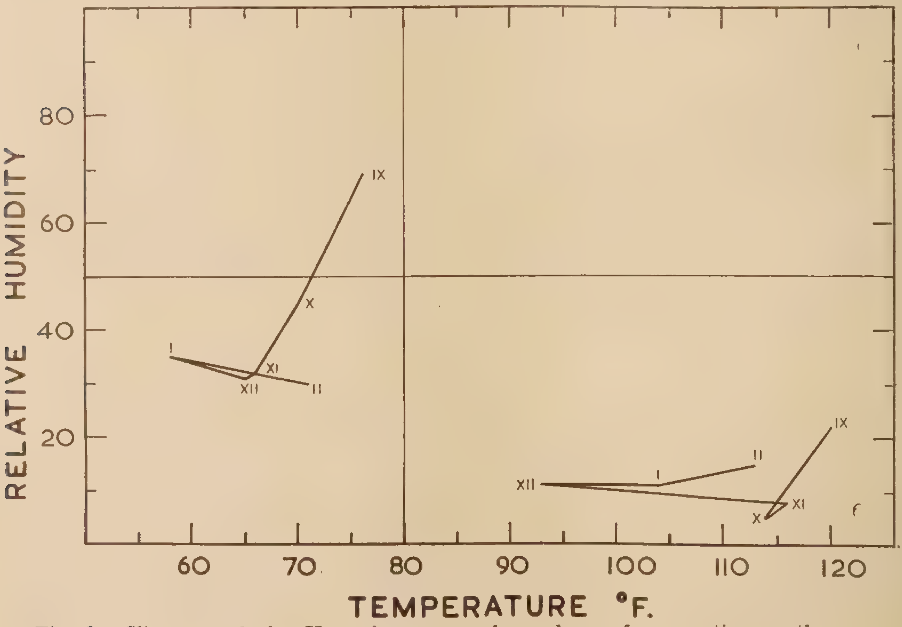

Fig. 2.—Climatograph for Kano for a normal warehouse from continuous thermo-hygrograph records taken about one foot under the iron roof.

These figures illustrate the range of conditions experienced by insects in the shady parts of pyramids. The conditions at dusk when most insects are flying or walking actively in the open approximate to points about midway between the maximum and minimum lines of fig. 1.

Thermorecorders and hygrorecorders were placed in a warehouse, on a box about one foot high, and kept continuously in operation. Monthly maximum and minimum temperatures and relative humidities inside a warehouse are plotted in fig. 3. These are the conditions experienced by insects at the periphery of the stack in a warehouse.

The bulk of the air in a warehouse is fairly uniform in temperature but in the top foot or two and bottom three feet or so there are distinct gradients. Thus at 11 a.m. in October on several days in one warehouse, temperatures taken at floor level were all 90°F. and at successive nine-inch levels above the floor were 94°F., 96°F., 98°F., 99°F. Near the roof the gradient is very marked for at 1 p.m. a temperature of 114°F. occurred at one foot below the roof and 140°F. two inches from it. Similarly, reversed gradients of temperature presumably occur at night, with temperatures one foot from the roof lower than that of the body of the warehouse.

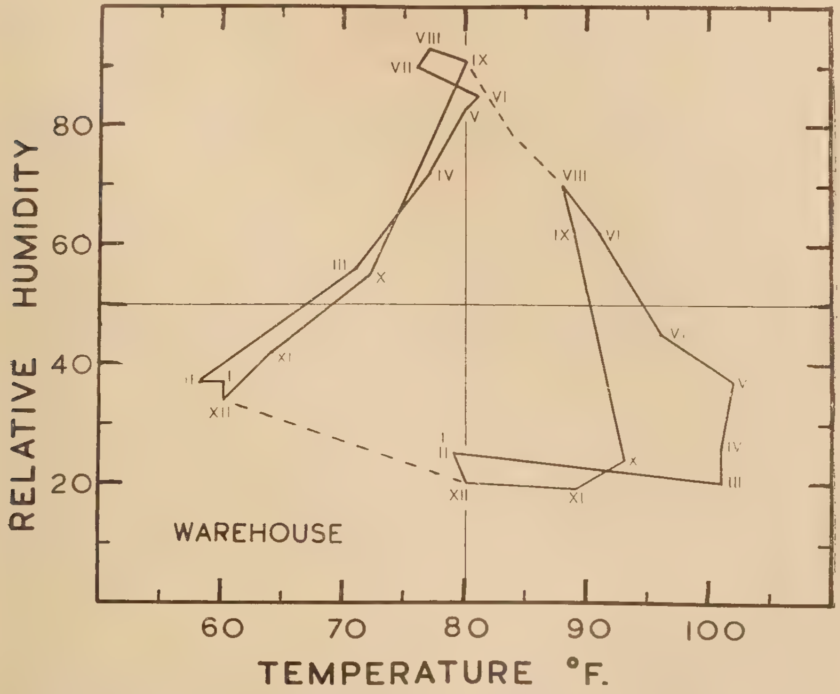

Fig. 3.—Climatograph for a normal warehouse in Kano from continuous thermo-hygrograph records taken about one foot above the floor.

Before the groundnuts are permanently stacked they are left exposed to the sun for long periods, for stacking is a slow process. In addition, each layer of bags in a pyramid is exposed for a period before the next layer is put on top of it. The nuts are, of course, also exposed to the colder night air, but work is rarely started until the morning air has warmed, so the sacks are usually stacked hot and dry.

Thermocouple ropes were placed in various positions in one pyramid and two warehouses ; these revealed the temperatures at the middle of the stack to be of the order of 40°C. (104°F.). These ropes were threaded between sacks, none passing through the nuts. One warehouse was known to be heavily infested by *Trogoderma granarium* Everts. The temperatures recorded by the one thermocouple rope passing through the stack in this warehouse remained fairly constant at just over 42°C. (108°F.). Five couples were placed in the other warehouse which was not affected by *Trogoderma* (Table I). This warehouse was loaded in April 1949. The temperature inside the stack was 41°C. (106°F.) in May and about 39·5°C. (103°F.) in September. Then in the harmattan season it fell and was about 27°C. in February shortly before the nuts were removed. The pyramid, containing six ropes, became heavily infested by *Trogoderma* although none was seen when stacking was in progress in December 1948. Excluding the couples recording the temperature of the pyramid plinth, which was always from two to five degrees centigrade cooler than the next couple 75 cm. above, and the couples at the surface of the pyramid, temperatures in this stack ranged from 39·9°C. (103·8°F.) to 45·5°C. (113·9°F.) in May, 37·3°C. (99·1°F.) to 44·0°C. (111·2°F.) in July and 39·9°C. (103·8°F.) to 46·8°C. (116·2°F.) in October shortly before railment. Table II gives the figures for three of the ropes only.

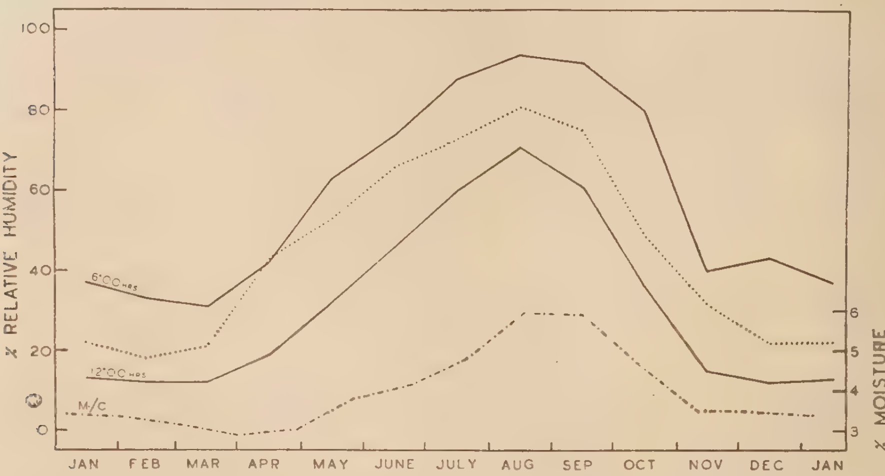

Fig. 4.—Relative humidity in Kano showing the monthly means of readings taken every 3 hours (dotted line) and the monthly means of values at 6.00 and 12.00 hours. The moisture content of samples of groundnuts taken at 4-week intervals is also shown.

Moisture content.

Groundnuts are usually very dry when they go into store, but they react rapidly to changes in relative humidity. A curve relating relative humidity and moisture content was obtained in the laboratory by keeping groundnuts in a thin layer in dishes at a constant humidity, maintained in a desiccator by sulphuric acid/water mixtures. This curve is given in fig. 5. A laboratory experiment carried out in atmospheric conditions in an outhouse gave a representative picture of the moisture changes in a small sample of nuts (Table III, col. 1). Details of the moisture content changes of groundnuts accompanying the relative humidity changes are shown in fig. 4. Groundnuts come to Kano for long term storage between November and April at a moisture content in the range 3·0 to 3·4 per cent., become as moist as 6 per cent.

in August and dry out again to 3 per cent. in March. The mean moisture content over a year's storage period in a small experimental bulk was 4·4 per cent., readings being taken every four weeks. For samples taken at the outside of a commercial stack in a warehouse the mean for a year was 4·3 per cent. (Table III, col. 2).

TABLE I.

Temperatures °C. in warehouse not infested by *Trogoderma* in 1949–50.

Position in stack		Rope 1	Rope 3	Rope 5
		Near bottom	Centre	Near top
Surface ...	May	38·4	41·5	38·2
Middle ...		41·1	40·8	41·7
Surface ...	Sept.	34·4	39·9	31·9
Middle ...		40·1	39·3	39·9
Surface ...	Feb.	25·0	25·1	25·5
Middle ...		29·0	26·3	26·4

Temperatures are given for the couple at the surface of the stack and for one of the eight couples inside the stack for three of the five thermocouple ropes built horizontally into the stack.

About one-quarter of the sacks in a stack are at the surface, and the remainder inside are subject to some lag in their reaction to humidity change. In addition, the high temperature in stacks causes some drying out in the centre so that a number of moisture values below 3 per cent., to as low as 2·3 per cent., have been obtained. This drying is accompanied by translocation of moisture (Kizel & others, 1939) to the bottom layer of sacks in the stack in contact with the relatively cool ground. This layer becomes very moist and mouldy and much of it is unfit for export. The moisture content of apparently sound nuts from this layer is often just over 6 per cent.

Samples for moisture determination have been taken from all parts of commercial stacks and the mean and range of figures is given in Table III (cols. 3–5). It will be seen that, in general, commercial samples are drier than would be expected from current humidities.

Differences between warehouse and pyramid storage.

The main difference between the conditions experienced by insects in warehouses and pyramids are in the temperatures and humidities as already described. Whilst internal temperatures in both are round about 40°C. (104°F.), the temperature at the surface of a pyramid is often much higher and is therefore lethal. The diurnal range at the periphery of a pyramid may be as much as 25°C. (45°F.) whereas in a similar part of a warehouse stack it would be only 6°C. (11°F.). This makes pyramid storage less favourable to most insect life.

Another important difference between warehouses and pyramids, at least from October to April, is in light intensity. Warehouses are continuously dark except in occasional small spots and are little disturbed between loading and unloading. Pyramids undergo the ordinary diurnal light variation when uncovered. When covered (mid-April to mid-October) there is permanent darkness, but the space

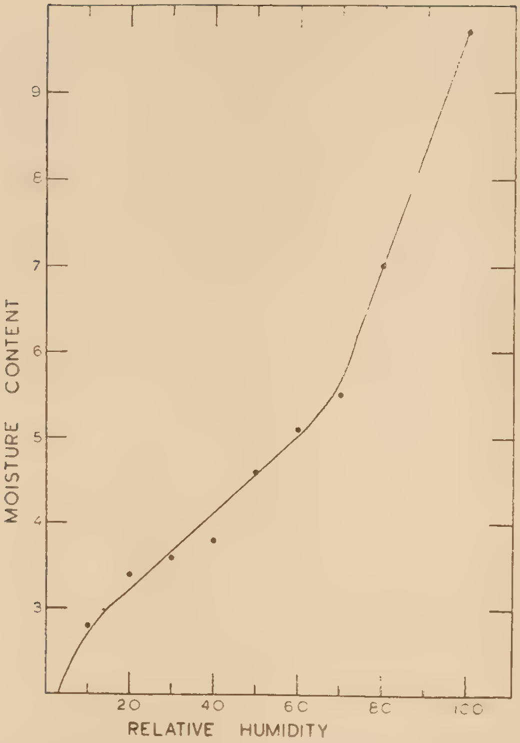

Fig. 5.—Curve relating moisture content per cent. of groundnuts to relative humidity per cent. of air.

TABLE II.

Temperatures °C. in *Trogoderma* infested pyramid in 1949.

Position		Base	2 m. up	5 m. up	½ m. from surface	Surface
Middle	May	36·5	41·9	40·6	41·9	43·2
Middle of SE side		39·3	45·5	—	43·4	42·9
Middle of NE side		37·7	40·4	—	40·4	40·9
M	July	39·8	43·5	42·2	43·6	40·7
SE		37·9	42·5	—	39·7	37·9
NE		37·2	41·5	—	37·3	37·3
M	Sept.	41·3	46·2	45·6	46·1	43·5
SE		40·3	46·8	—	43·1	42·4
NE		41·0	44·9	—	41·4	42·6
M	Oct.	40·8	45·9	45·8	43·4	42·5
SE		39·3	44·7	—	42·8	42·3
NE		40·7	44·9	—	42·0	41·1

Temperatures are given for three of six thermocouple ropes built vertically into a pyramid. These ropes were built in at the geometric centre of the base and at the geometric centre of two of the sloping faces of the pyramid. Temperatures for four or five of the nine thermocouple positions on each rope are recorded.

available for free insect movement is restricted by the rick sheets, and the temperatures encountered are high. Heavy insect damage in pyramids often occurs where nearby trees protect the pyramid from direct sunlight.

So long as storage of old crop nuts lasts until new nuts arrive, insect harbourage in empty warehouses is not important in infesting the new crop. It is worth noting, however, that most warehouses contain many cracks and crannies for carrying over pest insects whereas pyramid plinths are unlikely to do so. Trees are also an important hiding place for warehouse insects. In general, it matters little where most warehouse insects hide since nearly all are able to spread to new storage sites by flight at dusk.

The Insect Problem.

The insects associated with stored produce fall into a number of broad categories. They may be (*a*) actual pests eating the produce, (*b*) scavengers, (*c*) feeders on moulds affecting the produce, (*d*) predators and (*e*) parasites of the foregoing kinds. A number of strays only present by accident are also found frequently. In northern Nigeria insects are active, and the distinction between storage pests and strays is not always obvious, especially as there is much open air storage. Storage pests are often found flying far from commercial storage areas and strays are often found in warehouses. Some insects such as ants are found in warehouses merely because they are nesting under the floor. This is also true for termites, but these are pests because they destroy sacking and cause spillage and wastage of the produce.

TABLE III.

Moisture content per cent. (estimated by drying at 102°C. for 3 hours) of samples kept experimentally under simulated field conditions and of samples taken from commercial storage.

Month	Lab. expt.	Outside of warehouse stack	Various commercial stacks		
			No. of stacks sampled	Mean	Range
January	3·4	3·3	4	2·8	2·3–3·3
February ...	3·3	3·1	—	—	—
March	3·0	3·2	—	—	—
April	3·0	3·8	—	—	—
May	3·8	—	30	3·5	2·8–4·5
June	4·1	—	24	3·6	3·0–4·2
July	4·8	5·3	12	4·3	3·4–5·0
August	6·0	6·3	9	3·9	3·5–4·3
September ...	5·9	4·0	21	4·6	3·4–6·1
October	4·6	3·8	3	3·6	3·0–4·9
November ...	3·5	3·2	29	3·4	2·9–4·3
December ...	3·4	3·2	13	3·4	2·5–5·5

For most of the year Kano is very dry (fig. 4) and only species able to withstand dryness are serious pests. From June to September, the climate is wetter and the numbers of individuals and species increase markedly.

Golding (1946) lists the insect pests of Nigerian crops including storage pests. The present paper includes one new major pest, *Trogoderma granarium*, and a number of minor insects not mentioned in that paper, marked (*) when first mentioned. The relative importance of each insect is assessed and notable absentees are mentioned referring particularly to species present in the south of Nigeria.

The species present.

1. LEPIDOPTERA.

Only the Phycitid moths, *Plodia interpunctella* (Hb.), *Ephestia cautella* (Wlk.) and *Corcyra cephalonica* (Staint.) are sufficiently numerous to be important. *Corcyra* is slow breeding and does not appear in numbers until groundnuts have been stored for a year or more but the other species are often numerous inside warehouses after only two months' storage. Both probably occur on farms for they affect a wide range of produce and fly actively at dusk. *Ephestia* has been found flying at a distance of fifty miles from any groundnut storage centre and *Plodia* larvae have been found on groundnuts arriving in Kano. Moth numbers increase rapidly in warehouses but open air pyramid storage does not appear to suit them. *Ephestia elutella* (Hb.) was not recorded in any part of Nigeria but Mr. G. A. Brett of the United Kingdom Ministry of Agriculture recorded it on a ship from Nigeria feeding on grain residues left from a previous voyage. From this it is inferred that these individuals did a round trip between England and Nigeria being some six weeks in tropical waters.

Ephestia kuehniella Zell. was not found in Nigeria. This is not surprising as it does not breed satisfactorily at 30°C. (Raichoudhury & Jacobs, 1937) and Nigerian temperatures are higher for most of the day. *Plodia* and *E. cautella* complete a generation in two months.

A few Tinaeid moths occur sporadically. Two unidentified species have been taken in Kano.

The Gelechiid, *Sitotroga cerealella* (Ol.), was found in all stored guinea corn examined.

2. HEMIPTERA.

The Lygaeid, *Aphanus sordidus* (F.), is common throughout Nigeria, having been found by the Survey in Kano, Yola, Warri and Lagos—*i.e.*, in all climatic areas. Corby (1947) found that the bug sucked the nuts and seriously reduced the oil content. No puncture marks were left but the nuts became wrinkled and light in weight. Damage was confined to the outer three inches of piles of nuts stored in bulk. In Kano, however, no damage appeared to be done to the nuts and it seemed possible that the bug was predatory. It occurred in enormous numbers around warehouse doors and pyramid bases, especially in rubbish, vegetation and damper places. Numbers fall off noticeably in the dry season. It did not live in laboratory cultures in which the relative humidity was low.

Corby states that the development cycle in Yola is two months.

Anthocorid bugs, which may be *Lyctocoris campestris* (F.)* and *Xylocoris flavipes* (Reuter)* are widespread but seldom numerous. These are predatory species which are susceptible to dryness.

3. COLEOPTERA.

The majority of stored produce insects are beetles. Some of those found are unable to attack groundnuts. These include the typical grain pests such as *Rhizopertha dominica* (F.) and *Calandra oryzae* (L.), which are common in guinea corn and are also found flying occasionally. An unusual discovery was that of single individuals of *C. granaria* L.* once at Kano railway station and once at the famine storage buildings. There is no likelihood of these being misidentifications of *C. oryzae*.

(*a*) Tenebrionidae. This family is the most numerous both in species and individuals. *Tribolium castaneum* (Hbst.), locally called the groundnut beetle, is the real long term problem of groundnut storage. It is present in huge numbers and although there is some apparent reduction in the dry season, there is obvious recovery in the wet season. Undoubtedly the overlap of crop seasons has been a major cause of the development of a large population, but *Tribolium* could live between seasons in grain, in residues in warehouses, under the bark of trees and in ordinary household and shop merchandise. This species is very widespread and occurs in groundnut buying stations and almost certainly on farms, for it has been caught in flight far from storage centres.

In Kano, and in the surrounding commercially developed storage areas nearby, *T. castaneum* constitutes almost the entire *Tribolium* population. On the other hand, only half of the *Tribolium* in samples obtained from Yola and other river area storage centres were *T. castaneum*. The majority of the rest were *T. confusum* Duv.*. A few specimens of *T. anaphe* Hinton were also found in the Yola area (Yola, Numan, Shellen). Both these species were found rarely at Kano. *T. anaphe* is a native Nigerian species and it seems probable that *T. confusum* is also (Hinton, 1948). Very likely the Indian invader (*T. castaneum*) is gradually replacing the native species ; this process is almost complete in Kano, but is still in progress at Yola where a much smaller quantity of European foods is imported.

The closely related *Gnathocerus cornutus* (F.) and *Latheticus oryzae* Waterh. were not found in Kano. The two species of *Palorus*, *P. ratzeburgi* (Wissm.)* and *P. subdepressus* (Woll.)*, were both found frequently in dense local patches of limited extent. The former was the more common. An unidentified *Palorus* sp. was also taken.

Alphitobius laevigatus (F.) was common, especially in the wet season, but tended to die out as adults in the dry season. Adults congregated around wet patches in warehouses and at the base of pyramids, especially under the rick sheets. *A. diaperinus* (Panz.) was not found in Kano or in Lagos.

Very rarely single adults or larvae of *Tenebrio* were noted. Two of the adults, surprisingly, were *T. molitor* L.*, some were *T. obscurus* F.*, but most were *T. guineensis* Imhoff, also collected on groundnuts by K. G. Smith in Lagos.

Other Heteromera found were a single unidentified specimen of a species near to *Tribolium*, probably *Lygia* sp., *Mesostenopa picea* Kraatz which occurred occasionally in quite large numbers, *Anthicus floralis* L.* found fairly often singly, an unidentified *Anthicus* sp. and *Formicomus pagnioni* Pic.

(*b*) Dermestidae. A second major pest is the Dermestid beetle, *Trogoderma granarium**. This was first recorded in Nigeria in December 1948 by the Survey, in guinea corn stored as a reserve for feeding school children and civil prisoners in Kano. This infestation was promptly eradicated but in January 1949 an infestation on stored groundnuts was discovered. Other discoveries followed rapidly, and it was obvious that *Trogoderma* was then too widespread to eliminate. It has since been found in groundnuts stored at Kaura Namoda 140 miles west north-west of Kano, and almost certainly occurs at other storage centres.

All the individuals found bore a very marked pattern of the *versicolor* type and might have been mistaken for that species. *T. versicolor* (Creutz.) itself, however, was not found. Species related to *Trogoderma*, *Phradonoma tricolor* (Arrow)* and *P. cercyonoides* Reitt.* were often found as single specimens, especially in association with nuts from the neighbouring French territories. These species can fly, whereas *T. granarium* cannot and since reports of " flying *Trogoderma* " were quite frequent, *Phradonoma* can be assumed to be quite common. *Anthrenus*, which might also be confused with *Trogoderma*, was rare only two adults of *A. vorax* Waterh.* being seen.

The only other Dermestid found associated with groundnuts was *Attagenus gloriosae* (F.)* which was frequently found as adults and larvae, up to a dozen at a time in warehouses and as single adults on pyramids.

Dermestes maculatus Deg. was very common in Kano where hides and groundnuts are stored side by side. *D. ater* Deg. recorded by Golding and by K. G. Smith in the south was not seen in Kano.

(*c*) Other families. Two species belonging to the Cucujid group of families are widely dispersed among groundnuts in Kano and extremely numerous in patches of limited extent. They are *Laemophloeus ferrugineus* (Steph.)* and *Oryzaephilus mercator* Fauv. Golding records *L. minutus* (Ol.) which has not been found among the Kano or Lagos specimens but was taken by Richards & Herford (1930) from Gold Coast cocoa. *O. surinamensis* (L.) was not recorded in Northern Nigeria by the Survey but Golding records it on dried bananas and K. G. Smith found it in the south on rice and imported biscuits. *Ahasverus advena* (Waltl) which is very common in the south was not seen in Kano even in the wet season. One unidentified Cryptophagid was taken.

The Trogositid, *Tenebroides mauritanicus* (L.), was widespread in small numbers, disappearing in the dry season. The Nitidulid, *Carpophilus hemipterus* (L.)*, was found rarely and *C. dimidiatus* (F.)* more often. They were usually taken in flight or immediately after flight. *C. humeralis* (F.) recorded by Golding was not seen.

The single individuals of the Anobiid, *Lasioderma serricorne* (F.), taken probably came from cigarettes which are commonly attacked. *Stegobium paniceum* (L.) was not found as it is probably unable to survive the high temperature. Two specimens of *Ptinus* sp. possibly *P. bicinctus* Sturm(*?) were found but *Gibbium psylloides* (Czenp.) found in Ijebuode and Lagos in the south was not seen.

A Thorictid, *Thorictus* sp.,* not at present specifically determined, was found in numbers on pyramids at Birniwa and Malummaduri some 160 miles east north-east of Kano, and is unlikely to have affected the groundnuts. Another, *Thorictodes heydeni* (Reitt.)* was frequently found in Kano in local patches.

No Clerids were found in Kano. *Necrobia rufipes* (Deg.) is very common and widespread in association with palm kernels in the south and Mr. K. G. Smith has recorded *Thaneroclerus buqueti* (Lef.)* there.

The Mycetophagid, *Typhaea stercorea* (L.), was taken in the wet season. Carabids, Histerids and Staphylinids, often found on pyramids, were not collected as they are unlikely to be more than scavengers or predators.

One Bruchid, *Caryedon fuscus* (Goeze), is a pest of groundnuts in shell and of shelled nuts stored in bulk in Yola. In Kano it is widespread, a specimen or two being seen every day at the end of the wet season and for another two or three months, *i.e.*, at harvest and the beginning of storage. It appears unimportant in Kano but no evaluation of its effect on seed was made. Golding records that it also attacks seeds of *Tamarindus indica* and *Prosopis africana*. The Survey found it attacking seeds of *Acacia arabica* stored for the pods which are used in tanning. Miss Herford (1935) gives *Cassia* sp. and *Colutea* sp. as host plants. This species is widespread over the whole groundnut growing area being a serious pest in the Gambia and in French colonies.

Several other Bruchids were taken but have not been identified. There are many other leguminous plants in the area and it is not clear if these other Bruchid species are likely to attack groundnuts in the future. None of the Bruchids listed by Golding, *Bruchus analis* F., *Acanthoscelides obtectus* Say, *Callosobruchus phaseoli* (Chevr.) and *Pachymerus lacerdae* (Chevr.), was seen in the north.

The Anthribid, *Araecerus fasciculatus* (Deg.), a pest of cocoa, coffee and maize, was not found in Kano.

4. Other Orders.

Crickets are often common around pyramid bases and warehouse doors ; they may be scavengers. Cockroaches are not common in association with groundnuts ; they fly very actively, however, and several species have been found in houses.

Termites are pests because they eat holes in the sacking. The use of cinders in pyramid plinths and of groundnut husk as a covering for plinths and warehouse floors has proved an effective countermeasure. Damage only occurs now to bags stacked so as to project beyond the protective layer of husk.

Thermobia sp. is very numerous in warehouses and under rick sheets covering pyramids.

No Dipterous pests or parasites were noted but the large number of Hymenopterous parasites included the Bethylids, *Holepyris hawaiiensis* (Ashm.), *Rhabdepyris zeae* Turn. & Wtstn., *Plastanoxus westwoodi* (Kieff.), *P. munroi* Richards, and *Cephalonomia tarsalis* (Ashm.,) the Chalcid, *Antrocephalus mahensis* Masi, the Pteromalid, *Lariophagus distinguendus* (Först.), and the Braconid, *Microbracon hebetor* (Say).

Factors affecting the presence of insects in Kano.

Since Kano is a commercial centre with a large trade both with Nigerian seaports and across the desert to northern Africa and the Sudan, all cosmopolitan species have ample opportunity of reaching Kano. The factors controlling entry are first the high temperature which prevents the entry of such species as *Ptinus tectus* Boield., *Hofmannophila pseudospretella* (Staint.) and *Stegobium paniceum* (L.), and second the low humidity which prevents several southern species from colonising the north. Some species requiring humid conditions become numerous locally during the wet season. Traffic on the trade route from the south has increased considerably in the last fifty years and is probably responsible for any new introductions. The desert trade route is of very long standing and any insect introduced by this avenue is probably well established by now.

The airport is well removed from storage areas and since aircraft are unlikely to deal much with foods liable to infestation, new pests are unlikely to be introduced by air.

Some supplies of food suitable for all types of store pests are available in Kano. The major pests of groundnuts are *Tribolium castaneum* and *Trogoderma granarium*. *Tribolium* is a long standing, ubiquitous, pest which flies and spreads actively at dusk. It is probably near the limits of its low humidity tolerance but multiplies obviously in the wet season. *Trogoderma* is not adversely affected by the low humidity, but since the adult does not fly it does not spread rapidly by its own powers. It has only recently been noted as a serious pest, probably depending on undisturbed conditions of long storage in dry conditions to overcome the competition of other species.

The moths, *Plodia interpunctella* and *Ephestia cautella*, are numerous in warehouses but thrive less well in pyramids. *Corcyra cephalonica* is only abundant in nuts stored for more than a year. All moths fly actively at dusk.

Under present conditions new groundnuts put into store readily become infested by *Tribolium*, *Ephestia* and *Plodia* which fly actively, and are extremely likely to pick up *Trogoderma* by some means. Buying centres are not liable to heavy infestation as nuts pass through quickly at the most unfavourable season for insects. Farms have not been examined but as *Tribolium*, *Ephestia* and parasites have been caught flying in bush before the opening of the buying season it seems probable that farms have some infestation in the crop kept back as food. Large infestations are picked up and developed only at storage centres and the crops leaving them for ports are a menace to the other crops stored there. Groundnuts pick up a few southern insects at port and may arrive in Britain infested by typically southern species such as *Ahasverus* and *Necrobia*.

Numbers, distribution and activity.

Insects are obvious in warehouses at any time of day, and may also be found under the rick sheets on pyramids, but they are only obvious in the open at dusk and at night. The timing and extent of dusk activity is variable and its connection with climatic factors is not obvious. Adult *Trogoderma* are the first to become active, somewhere about 16.30 hours ; about an hour later moths begin to fly and shortly after this *Tribolium* adults begin to walk and by 18.00 hours they start flying. The period of flight is very variable often continuing for hours, sometimes ending in half an hour. Wind speed is obviously important and heavy rain, of course, makes flight impossible in exposed situations, though it is still attempted.

Tribolium and the moths come to lighted houses at all times of the night. Parasites and minor pests also become active at dusk. The time of dusk varies from about 18.00 hours to 19.30 hours local time.

The density of flying insects is greatest near the ground at dusk and falls off towards the top of pyramids and warehouses. Moths may fly indoors at any time. Handling of nuts stimulates flight of moths and beetles and increases the dusk activity.

No insects were seen on uncovered pyramids, on the outside walls of warehouses or on the outside of rick sheets during normal daylight with the exception of *Trogoderma*, the larvae of which may be seen if the insect is numerous.

The peripheral distribution of *Tribolium* adults in warehouses and the tendency to collect in wall-angles and corners was very obvious. Total numbers were so much above those economically permissible that the effect of a control measure was ascertained without recourse to the estimation of numbers.

The normal peripheral distribution of insects is reinforced in groundnut stacks by the abnormal internal stack temperatures. *Trogoderma* is the most resistant to prolonged high temperature and is the only species found at all commonly inside stacks. Slow building of stacks ensures that all sacks are invaded by flying adult insects during stack construction ; although most of these fly away again next day, they presumably lay eggs, giving rise to a generation that either migrates or dies.

TABLE IV.

Numbers of insects caught in a plate of water and a plate of soap solution in approximately 24 hours in six warehouses on the same day.

Position in warehouse	*Tribolium*	*Laemophloeus*	*Ephestia*	*Plodia*	Parasites	Bugs
In doorway	2,308	7	20	73	49	22
Near door (less than 1 foot away)	2,314	22	62	48	33	10
Near door (1 yard away against stack) ...	382	1	91	38	7	1
In central gangway (6 feet from door) ...	211	10	90	21	2	—
Away from door and wall but near stack in cool concrete store ...	181	3	81	10	10	—
Away from door and wall but near stack in hot iron store ...	102	3	93	169	5	—

Trogoderma found in the middle of stacks must either have moved into the hot region from the outside, which is unlikely, or have been introduced into the sacks before stacking.

Methods of estimation of numbers were not very successful and led to a very large amount of work. The methods considered were (*a*) the number per kg. of nuts in a sample taken from a sack with a standard Nigerian sampling spear, (*b*) the number found on foot square areas of wall, floor, sack, etc. and (*c*) the number caught in a water or soap solution trap left overnight in a warehouse.

The use of a sack sampling spear gave erratic results, due to variations in the distribution of beetles inside the sack and also to the insects clinging to the sack which escaped. This method was used in one warehouse which was sampled regularly and gave results ranging from 19 to 204 per kg. The range for samples from the same bags on the same day was 66 to 196, figures that are believed to be low.

The use of foot square areas of surface was not given a satisfactory trial. It proved difficult to count larvae on sacking surfaces and insects on walls were very active and numbered thousands. There was also the difficulty of distributing sample areas between floor, wall, corners, ceiling, rafters, doors and sacks but this problem was never faced owing to the large numbers of insects. Another difficulty was the rapid change of visible numbers at dusk and the variation in time of the peak.

Traps of water or soap solution were used in soup plates with about 40 sq. in. liquid surface. These were left in warehouses for an entire 24-hour period. Those left in the open evaporated quickly or were drunk by animals. The difficulties met in using these were the limited floor area available, and the tendency of plates put on sacks to slip off. At the time, it was more or less impossible to put two plates in equally attractive positions in a warehouse and a large difference between the catch for the two plates put in each warehouse was generally noted. Insects were removed by filtering the liquid through ordinary filter paper. Since the soap solution was very slimy and did not evaporate much more slowly than plain water there seems little advantage in its use. Table IV gives the catches in six warehouses on the same day and illustrates well the peripheral distribution.

Nowadays the groundnut agents have been persuaded to stow their nuts in the warehouse with an ample gangway around the stack and it should be possible in future to make a serious attempt to use either water traps or sample surface areas as a means of estimating insect numbers.

Of the moths caught and recorded in Table IV, only 30 per cent. of the *Ephestia* and 43 per cent. of the *Plodia* were male. In similar observations made in a cocoa-palm kernel warehouse in Lagos on eight days over a period of 3 weeks, only 24 per cent. of 350 *Ephestia* were male ; no *Plodia* were captured.

The Trogoderma *problem.*

The occurrence of *Trogoderma granarium* in stored foods in Nigeria presents some novel problems which are now considered in more detail. The climate of northern Nigeria is well suited to this insect, being warm and dry and comparatively unfavourable for much of the year to most other storage insects. Yet this species was not apparently noticed before December, 1948, when it appeared in an enormous outburst that was extremely obvious.

All the countries bordering the Sahara are suitable climatically and it is known as a pest in the Anglo-Egyptian Sudan (Oxley, 1950). The Ministry of Agriculture Infestation Division in the United Kingdom recorded it in two shipments from Dakar, French West Africa in 1944. The Commonwealth Institute of Entomology in 25 years have received specimens from the Sudan on eight occasions, from Kenya once in 1948, but never before from West Africa. The infestation Division records of the species from Nigeria commence in January, 1948, excluding a record of a single dead adult in March, 1946 ; unfortunately the Survey was not aware of the twenty-five records of infested shipments in 1948.

It was also unfortunate that the Survey selected uninfested stores for experimental observations and that a number of badly affected stocks were railed without the Survey knowing until examination of the empty warehouses later revealed the fact.

From the Infestation Division records quoted above, it is evident that the 1946–47 crop was infested and it is likely that the 1944–45 crop may also have been affected just badly enough for the one adult to reach England. The Hausa has a word for the insect which infers that it occurs in long stored food and since he has words for few insects (the ubiquitous *Tribolium* also has a name), this suggests that *Trogoderma* is well established in Nigeria. This is to be expected in view of the long standing cross desert trade with the Sudan. Also the occurrence of the beetles in guinea corn, stored as a famine reserve away from groundnuts, supports this contention.

If *Trogoderma* is accepted as endemic to Nigeria, it is necessary to explain why it has gone unnoticed for so long. This is in part due to the absence of entomologists from the area and to the unfamiliarity with insects of those handling nuts. Thus for example in December, 1948, nuts were railed which were so heavily affected that the typical *Trogoderma* damage to sacks was obvious, but it was ascribed to heat. In any case, the population of *Trogoderma* has increased remarkably in recent years. Two factors contribute to this, the increased period of storage and the steadily rising price of groundnuts. Before 1940 groundnuts were all railed by April of each year, but in 1946 there were some left in November when the following crop was harvested. Since then there has been crop overlap each year and nuts have often remained in store for some eighteen months after harvesting. When in store the crop is comparatively undisturbed, and at a favourable temperature for the insects to multiply quickly. If *Trogoderma* is endemic in Nigeria and occurs in the farms, it is likely that it is often brought to the storage centres in small numbers and, with long storage, is able to multiply into enormous populations. Rising prices acted in the beetles favour by making it a safe business proposition to retain nuts from one season for sale the next as the price was fairly certain to rise. This is a perfectly legal practice but provides another year for the *Trogoderma* in which to multiply. Petty theft of nuts from storage sites and the sale of these nuts mixed with new crop have also increased the numbers of *Trogoderma* in nuts at the commencement of storage.

The handling between harvest and final storage probably kills many adults and larvae, and *Trogoderma* is rarely visible on nuts arriving at a storage centre. One pyramid built in December, 1948, and much used for experiment was eventually badly infested but none were seen during loading. On the other hand from February, 1949, onwards, several warehouses were found infested shortly after loading. The origin of the groundnuts in store was traceable on only one occasion, in a small warehouse containing about 240 tons. This quantity was received in twenty-one batches from nine buying centres in half a dozen widely separated areas. There was thus no chance of establishing whether or not the insect originated from a localised area, but this is not very likely.

Only two buying agents, one buying on a large scale, have so far kept free of infestation.

Nuts from French West Africa were on the whole free of *Trogoderma*. This might be due to the absence of the insect from French territories but is more likely to be due to the disturbance of a long slow journey to Kano, often by camel, and a shorter storage period in Kano.

Although the evidence points to Kano storage in the first place having been infested by the introduction of infested nuts, during 1949 cross infestation in Kano rapidly became of major importance. It is extremely difficult, if not impossible, to be certain whether infestations discovered late in storage are due to the build-up from very small original populations or due to cross infestation, but fairly reliable opinions were formed on infestations discovered before May. Among these were some instances of nuts being loaded into warehouses known to have housed infested stock the previous season, some where the warehouse evidently had contained infested stock the previous season, although it was not known before loading and at least one instance where the crop of two seasons earlier had been infested, the warehouse having been unused for some six months. Other new groundnut stocks became infested through being handled in close proximity to old infested stock or to infested premises and some because old stocks were stacked against them prior to railment. Since most warehouses in Kano have an abundance of cracks in walls and woodwork, it is difficult to remove *Trogoderma* once it has gained access.

Other methods of cross infestation also play a part. Since the adult does not fly, *Trogoderma* does not spread far of its own accord but larvae do crawl to adjacent storage sites. This is often aided by wind for both adults and larvae are readily blown. In any event it is common practice to screen spilled nuts from warehouse floors and pyramid plinths to remove dirt, dust, and husk. This is usually done in the open and no doubt some insects are blown away with the dust.

Clothing may also be a significant cause of spread for labourers rest their gowns on infested sacks when they work, and clerks and inspectors for instance often get nuts and insects in shoes, trouser turn-ups and note-books. The carriage of infested nuts to a central fumigation station in open lorries almost certainly spread the insect all over Kano.

Evidence that cross infestation occurs is given by the experience of one agent who believed in ventilating his stores by opening the doors daily. Many of his nuts were infested only in the warehouse doorways, whence *Trogoderma* may have been carried by the wind.

During the past year or two *Trogoderma* has frequently been taken by rail to the ports at Port Harcourt, Apapa and Baro, and from Baro by river to Warri and Burutu. Experiences in India, quoted in a letter from Dr. Sontakhay, suggest that if this flow continues *Trogoderma* might eventually become established at the ports. So far, however, *Trogoderma* has not flourished in the cooler, damper coastal climate. This was thought to be due to the more severe competition exercised by *Tribolium* in such conditions and experiments in Lagos show that this is partly true. K. G. Smith has found in addition, however, that it is also due to predation in humid conditions by an Anthocorid bug, probably *Lyctocoris,* which is unable to withstand dry conditions.

Trogoderma is little affected by relative humidity, although its optimum is about 80 per cent. Its optimum temperature is about 35° to 40°C. (fig. 6). In Kano, each generation takes about six weeks and each female is capable of laying over 50 eggs in a life of less than a fortnight. Generations tend to keep in step and outbreaks appear in places which are too hot for other species—*i.e.,* across the top of a stack just under the iron roof of warehouses. *Tribolium castaneum* is known to develop satisfactorily at 30 per cent. R.H. but it does much better at higher humidities. The optimum temperature for this species is between 30° and 35°C. (fig. 6).

There seems little to choose between open air storage and warehouses in relation to *Trogoderma* infestation since this insect is not deterred by the high temperatures at surfaces and inside stacks. Open air storage is much more liable to casual cross infestation but many of the warehouses in Kano cannot be used as they are known to be infested.

Individually each *Trogoderma* probably does more damage than a *Tribolium.* The larva is a dirty feeder, powdering more nut than it eats so that it causes a higher proportion of powdering than *Tribolium.* In addition, it forms much denser pockets of infestation. In these dense pockets there appears to be a great deal of movement in and out of sacks which results in a form of damage to sacks which is typical of *Trogoderma.* This gives rise to a weakening of the sacks, especially where two sacks touch, finally resulting in tearing.

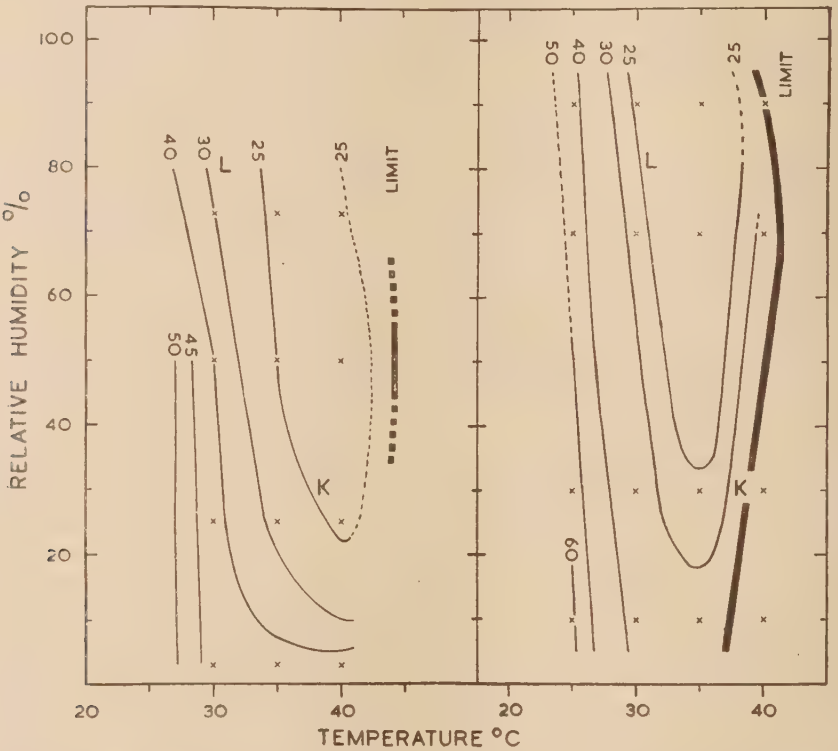

Fig. 6.—Temperature humidity diagrams for *Trogoderma* (left) and *Tribolium castaneum* (right) with wheatfeed as food. Crosses mark temperature humidity combinations at which experiments were done. The lines join points where the total life-cycle (egg laid to adult) in days are equal. [Figures given for *Trogoderma* agree closely with those given by Hadaway using malt as food in a London University thesis, 1940.]

K = Internal stack conditions in Kano.
L = Warehouse conditions in Lagos.

The Tribolium *problem.*

The problem of *Tribolium* infestation contrasts strikingly with that of *Trogoderma. Tribolium* has been known as a storage pest in northern Nigeria for many years, especially in groundnuts and guinea corn. It is so well established that the extension of storage of groundnuts into the wet season in recent years, followed by a further lengthening of storage so that the crops of two years were stored side by side, caused an enormous increase in numbers.

The adult is very conspicuous, and spreads very rapidly by flight, particularly at dusk. As a result, newly stacked groundnuts at storage centres are infested immediately. Handling greatly increases activity so that breakdown of a stack disperses its population amongst others in the vicinity. Cross infestation might be restricted a little by screening warehouses but there seems to be little prospect of preventing the spread of this insect. Therefore reduction of the adult population by spraying offers the best means of combating this pest.

The larva of *Tribolium* is inconspicuous ; it develops quickly in about six weeks, whereas the adult lives several months, and it burrows into nuts while feeding. It seems probable that the rate of cannibalism in developmental stages is high.

At port, *Tribolium* spreads to other export crops but does little damage to either cocoa or palm kernels.

Losses.

Losses in groundnuts stored in Nigeria can be considered under three headings (1) weight losses (2) depreciation in quality and (3) monetary expenditure incurred as a result of the presence of storage pests.

Sampling.

Before the problem of estimating losses could be investigated, however, some satisfactory sampling methods had to be obtained.

Produce examiners in Nigeria sample bags of groundnuts at railment with a conical sampling spear 1 ft. long and 1½ in. in diameter. This has a pointed solid tip and an aperture to receive the sample occupying most of the length and about a quarter of the circumference of the sampler. The examiner hits the bag at the point to be sampled with the base of the sampler to part the fibres of the bag. The point is then forced between fibres and the spear pushed about one half of its length into the bag. Nuts enter the sampler and the required amount of sample can be run out of the open base into a container for examination. The hole left in the sack is closed by rubbing the fibres together with the base of the sampler.

Since this instrument is in widespread use in Nigeria it seemed an ideal instrument to use for sampling, so a critical examination of its use was made.

The purposes of sampling were to obtain estimates of the proportions of whole, half and broken pieces of nuts, the amount of dust and foreign matter and number of insects present in the bag of nuts sampled. The factors likely to cause this method to give false results are :—

(*a*) breakage of nuts by the banging of the sack at the sampling point and by the point of the sampler,

(*b*) separation of whole and broken nuts into layers in the bag ; this is obvious where nuts are scattered over the floor of stores as a result of bag breakage, while the filtering of dust through the meshes of the underside of sacks is also obvious,

(*c*) selective sampling resulting in the sample not giving a true picture of conditions at the sampling point. Insects are comparable in size with the smaller broken pieces and behave like them when dead. Since live insects tend to be commonest at the periphery of a sack but cling to the sacking or to nuts, a reliable guide to insect numbers is unlikely to be achieved from such samples.

Three experiments were performed using this sampler. In the first, samples were taken with a spear sampler from seven points in a sack of whole nuts and, immediately after taking each and before closing the sample hole, a sample was taken inside the sack from as near as possible the same position with the cupped hand. The spear samples contained altogether 2,507 whole nuts, 144 splits (=72 whole) and 43 fragments whilst the hand samples contained 2,217 whole nuts, 196 splits (=98 whole) and 65 fragments. Thus the spear samples contained 2·8 per cent. and the hand samples 4·4 per cent. of nuts broken by sampling.

TABLE V.

Percentage of dust in samples from various levels in sacks.

Set	Sample position	Per cent. dust	
		Passing 30	Passing 10 Not passing 30
A	Top	0·7	2·4
B	Middle	2·0	3·9
C	Bottom	7·4	9·6
D	Top	1·0	1·7
D	Middle	1·3	3·1
D	Bottom	5·3	7·4

It is clear, therefore, that the beating of sacks before sampling breaks nuts. Since more split nuts were found in hand samples it could be concluded that the spear tends to reject some of the splits but this is unlikely. It is more likely that the spear point entering the sacks splits more nuts around the spear which do not fall into it and that hand sampling causes further splitting. Therefore about 3 per cent. of the whole nuts present may fairly be said to be split into halves by the sampling process and fall into the sample spear.

In the second experiment whole nuts were remixed with split and broken nuts as homogeneously as possible by weighing one pound lots of whole nuts and one pound lots of mixed broken and split nuts, putting them alternatively into a clean new sack. This sack, known to contain 50 per cent. whole nuts, was sewn up when full but otherwise was handled as little as possible. Five laboratory assistants immediately took two or three samples each with the sampling spear from different zones of the sack and sorted them. The sack mouth was unstitched and four assistants each took one hand sample close to his original sampling points.

The mean percentages by weight of whole nuts and splits in twelve spear samples were 44·7 and 27·8 compared with 42·3 and 31·8 for four hand samples. A difference between spear and hand samples was found again but the breakage of whole nuts was apparently greater in this experiment, being over 5 per cent., that is, over 10 per cent. of the whole nuts present.

The mouth of the sack used in the last experiment was resewn. The sack was moved about and handled, taking care not to use it too roughly and to keep the unsewn end consistently uppermost. Then it was laid flat and reopened at the sewn end and nuts removed in approximately 4 lb. lots. These were sorted as taken. The percentages by weight of whole nuts in successive quarters of the sack were 44·6 (sewn), 47·4, 47·2, 51·9 (unsewn). This indicates that whole nuts tend to come to the top with handling. It also suggests that a middle sample gives a good indication of the true proportion of whole nuts since the mean for the whole bag proved to be 47·8 per cent. with 28·5 per cent. splits and 23·7 per cent. broken fragments.

This experiment gives a 2·2 per cent. fall in proportion of whole nuts—a loss of 4·4 per cent. of those originally present. Since this is partly due to handling, this experiment confirms the results of the first experiment rather than those of the second. It must be concluded that the discrepancy in the second experiment was due to the selective sampling of pieces, possibly due to their falling between the whole nuts into the spear ; in that experiment 44·7 per cent. whole nuts were obtained when at least 47·8 per cent. were present. It is obvious that a personal factor will influence the result depending on how much the sampler moves his spear. The proportions of whole nuts obtained in the spear by the five laboratory assistants in the second experiment were 48·4, 44·4, 43·5, 43·4 and 42·9 per cent. Summarising, it may be said that sampling with a spear breaks 4 per cent. of the whole nuts present, and that the spear sample is further biassed to give a final result some 10 per cent. low for whole nuts.

Since dust was excluded from these laboratory experiments, field samples were utilised to test the segregation of dust. One set of 25 sacks from various points in an exposed surface of a stack were sampled at the top, another from the middle and a third at the bottom. A fourth set was divided into three groups sampled at top, middle and bottom respectively, each group of samples being kept separately. The results (Table V) show clearly that dust filters to the bottom of the sack. The standard position adopted for sampling with a spear was the middle of the exposed face of a sack. These results show that it is probable that only about half of the average weight of a dust passing a 30-mesh to the inch sieve is obtained at this point.

On the basis of these tests it was decided that whole sacks must be used as units in experiments designed to estimate weight loss but that spear samples could be used for quality tests.

Weight loss.

Changes in weight of stored groundnuts are due to (*a*) the change in moisture content of the nuts, and (*b*) the feeding of insects and other storage pests.

(1) Moisture content.

As has been mentioned earlier (p. 117) the average moisture content of groundnuts stored for a year in Kano is about 4·4 per cent. Some very wet nuts are discarded as unfit for export. Thus, since the average moisture content was 3·4 per cent. when put into store, the average increase in moisture content during storage is about 1 per cent., or nearly 2 lb. per sack. Nuts railed over the period January to April are dry and may show a loss of about 6 oz. per sack ; those railed in August may show a gain of about 3 lb. 8 oz. The maximum gain noted in practice in a commercial stack of some 750 tons was about 2 lb. 8 oz. per sack.

(2) Losses due to storage insects.

Whole groundnuts are soft and easily attacked by insects but even so, broken pieces appear to be attacked more easily. In a series of laboratory experiments in which twenty-six 50-gm. samples of nuts were exposed to 200 adult *Tribolium* for various periods between 4 and 52 weeks, the total losses in 13 samples of each were : whole nuts 52·1 gm., broken nuts (including splits) 73·1 gm.

Since it is important to know the extent of losses under field conditions before trying to prevent them, a number of experiments were set up to obtain this information. The problem was extremely complex, having many foreseen and unforeseen difficulties. The storage sites chosen were a representative selection, except in relation to *Trogoderma* infestation which was not predictable at the time experiments were started. All experiments were carried out under normal commercial storage conditions and most lasted from nine to twelve months. Holed and weak sacks so often used commercially were scrupulously avoided.

Damage was estimated directly in terms of weight losses, but, in addition, all the fine powder and fragments normally shipped were also considered as loss. Five sacks grouped closely together were taken as units and weighed, the dust formed in these five sacks during storage being sieved off and weighed at the end of the experiment.

At the commencement of storage, nuts contained no fine dust but very rarely as much as 1 per cent. of testa and small fragments was removed. Insect activity and handling increase the amount of testa and fragments during storage and insect feeding produces more powder and frass. A 30-mesh to the inch sieve was available and was used as an arbitrary division between frass and very small fragments. It was found that, in general, about half of the dust passing a 10-mesh sieve would pass a 30-mesh. Rather less of the dust was frass when small amounts of dust were obtained (less than 2 per cent.) and rather more when large quantities of dust were present (over 4 per cent.). When dust was obtained in field experiments using a 12-mesh sieve, it was found that a minimum of 60 per cent. of this dust was frass, the remainder being testa and fine fragments.

TABLE VI.

Summary of estimates of weight loss in groundnuts during storage (as percentage original wet weight).

Site	Duration of storage	*Trogoderma* infestation	Position of sacks	No. of sacks	Wt. of dust found %	Total loss %
Pyramid A ...	11 months	Absent ...	Outer...	30	2·0	* 3·6
,, B ...	12 ,,	Slight ...	Outer...	50	1·8	2·5
,, B ...	12 ,,	Slight ...	Outer bottom layer...	20	3·9	6·6
,, B ...	12 ,,	Slight ...	Outer bottom layer...	60	?	11·9t
,, C ...	10½ ,,	Heavy ...	Outer...	50	2·1	4·0
,, B ...	12 ,,	Slight ...	Inner...	50	1·6	2·0
,, B ...	12 ,,	Slight ...	Inner bottom layer...	70	1·4	? w
,, C ...	10½ ,,	Heavy ...	Inner...	50	1·2	1·8
Warehouse D	9 ,,	Absent ...	Outer...	36	3·2	4·6
,, E	10 ,,	Absent ...	Outer...	10	2·4	5·0
,, F	10 ,,	Very heavy	Outer...	39	3·6	7·1
,, G	6 ,,	Absent ...	Randomised... ...	16	2·6	2·9
,, D	9 ,,	Absent ...	Inner...	42	1·7	2·4
,, F	10 ,,	Very heavy	Inner...	51	2·8	4·3
,, H	8 ,,	Absent ...	Outer...	15	5·3	** 5·1
,, J	7 ,,	Heavy ...	Outer...	60	3·3	5·5
,, K	7 ,,	Heavy ...	Outer...	75	2·9	3·3
,, H	8 ,,	Absent ...	Inner...	15	2·9	3·8
,, J	7 ,,	Heavy ...	Inner...	65	2·7	4·8
,, K	7 ,,	Heavy ...	Inner...	45	2·5	4·9

*Adjusted and **not adjusted to moisture change. t=loss due to spillage caused by termite damage to sacks. w=caking due to water damage prevented accurate estimation.

From laboratory experiments, using lots of 200 *Tribolium* adults in jars containing 50 gm. nuts, either whole or broken, it was found that only 46 per cent. of the dry weight loss was recovered as frass. The remainder was presumably dissipated as carbon dioxide and water vapour. Hence in the field it would be expected that half the true weight loss would appear as dry weight loss and the other half as groundnut dust. Some of the dust inevitably escapes through the interstices of the sacking and that obtained by sifting through the 10- or 12-mesh sieve used in field experiments would be mixed with about an equal weight of testa and small fragments. Thus, the total weight of dust passing the 10-mesh sieve gives a minimum estimate of weight loss and twice the dry weight loss observed gives another estimate. In this paper the small fragments passing a 10-mesh sieve are also regarded as a real loss and the estimate accepted as minimum when available is the sum of dry weight loss and weight of dust.

Three main types of field test were performed. In the first, sacks were weighed before storage and again after storage, when they were also sieved through a 12-mesh sieve to determine the quantity of dust produced. Moisture measurements were taken at beginning and end of storage. This kind of experiment was made in three pyramids (Table VI, A–C) and four warehouses (Table VI, D–G). Two of the pyramids and one warehouse became infested by *Trogoderma*. Weighed sacks were placed in the outer layers and the centre of the stacks and at various levels. Sacks placed in the bottom layer of stacks were largely spoiled by the variable moisture changes and in the pyramid also by termite damage. Storage periods were 10½, 11 and 12 months in pyramids and 6, 9 and 10 months in warehouses.

Table VI gives a summary of losses grouped according to *Trogoderma* infestation and to position in the stack. Average overall loss was 4–4·5 per cent., including 2·5 per cent. of dust.

The second type of experiment was the same as the first except that no original weighings or moisture estimations were made. It was assumed that the original weights of sacks were standard but it is likely that there was some deficit. The mean deficit for sacks at the beginning of the first kind of experiment was only 4 oz. but the presence of Survey officers probably accounted for this. These experiments were carried out in three warehouses (Table VI, H-K). Two of these were *Trogoderma* infested and storage lasted seven months. Storage in the third was for eight months.

The overall figures for this kind of experiment show a mean weight of dust of 3 per cent. (5 lb. 8 oz. per sack) and a gross weight loss of 2 per cent. (4 lb. 1 oz.). The sum of these figures are slightly higher than that obtained from the first kind of experiment. This is partly because these results are not corrected for moisture changes, the nuts probably being a little drier when railed than when stacked, since they were loaded in April and unloaded in December to January. Also the original weight of the sacks was probably a little below standard.

The third type of experiment performed by L. A. W. Hayward involved sieving of nuts while stocks were being railed. Samples were taken from sacks as stored in all parts of the stacks, from nuts spilled on the warehouse floor or pyramid base, and from sacks into which nuts were being rebagged from the floor. The mean percentages of dust in samples from two pyramids were 2·9 and 3·4. For six warehouses percentages were 4·75, 5·1, 4·1, 3·1, 4·8, and 5·1. For the last two warehouses, figures for ordinary sacks were 4·7 and 4·8, for rebagged nuts 7·0 and 11·5, and for nuts still on the floor 13·4 and 12·0.

The mean percentage dust obtained was 3·15 for the two pyramids and 4·5 for the six warehouses. These figures represent minimum insect losses for these premises, and may be compared with the 2·5 per cent. and 3 per cent. of dust found in the two previous kinds of experiment, in which total losses were 4·5 per cent. and 5 per cent. respectively.

The first two types of experiment show that more dust was found in outer sacks than in inner ones. This was also shown by an experiment in which various sacks were sampled at a standard point using a spear. The sacks were selected from the face of a pyramid exposed during railment. Dust from the sacks in percentages by weight of the samples, working from one outside sack across the middle to the opposite outside sack, were : 0·59, 0·52, 0·44, 0·57, 0·35, 0·14, 0·93, 0·39, 0·49, 1·49. As pointed out earlier spear samples give low estimates of dust if taken in the standard position in middle of exposed face of sack.

The experiments described above show that, in general, the presence of *Trogoderma* in both warehouses and pyramids results in heavier damage. When the first infestation of groundnuts by *Trogoderma* was discovered a rough check was made on damage and in this extremely heavy infestation, a weight loss of 3 per cent. was estimated with 17 per cent. of dust remaining in the nuts. Official estimates of damage due to *Trogoderma* for 1947/8 crop were only about 0·1 per cent. of the crop and for 1948/9 about 0·5 per cent. in spite of a tendency to add other losses. These estimates are obviously much too low and do not, in fact, exceed those due to fire, theft and so on.

(3) Increase of weight in transit.

An increase of weight is to be expected after nuts leave Kano for the port. Large stacks are broken down in Kano and loaded in small units (240–300 sacks) in railway wagons which are broken down again and stacked at the port where moisture content records are higher than for Kano, ranging from 4 to 8 per cent. Relative humidity in Lagos may be about the same as Kano in August but from November to April it may be as much as 60 per cent. higher (fig. 7). Over a year this is equivalent on average to a 2½ per cent. increase in moisture content. Two experiments to illustrate this point were performed in January and February 1950 but the gain in weight was only 0·75 per cent. This was obviously due to freak harmattan conditions producing abnormally low humidities in Lagos on both occasions.

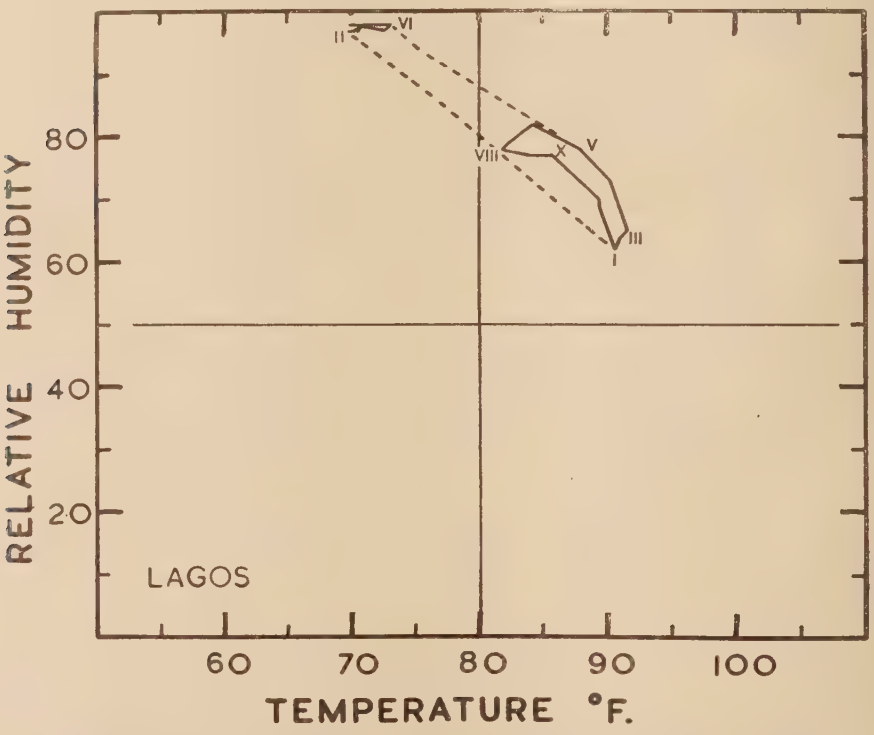

Fig. 7.—Climatograph for Lagos from ordinary meteorological records (*cf.* fig. 1).

(4) Losses due to termites.

Termites appear to do no direct damage to nuts, but they eat holes in the sacks if given the opportunity and so cause spillage and consequent loss. The use of cinders or groundnut husk on warehouse floors and pyramid plinths is an effective deterrent and restricts damage to the outside of pyramids. Even here it is caused through stacking sacks in such a way that they project beyond the protective layer of husk. In one experiment affected by termites for this reason, 60 out of 88 sacks were attacked and 10 per cent. by weight of the nuts lost ; the attack extended up seven layers and damage to the whole pyramid was of the order of 1–2 per cent. loss in weight. Only one or two pyramids a year are badly affected.

(5) Losses due to mammals.

Little damage seems to be caused by rodents. Hedgehogs are common in warehouses and under the rick sheets of covered pyramids. Although normally insectivorous it seems possible that they may eat a lot of spilled groundnuts, for one family ate the contents of one sack kept in a locked store at the laboratory.

Quality depreciation.

(1) Water damage.

Most of the admitted damage to groundnuts in storage is water damage. When badly affected the nuts cake, become mouldy, turn black and begin to rot and smell. The blackened nuts are obviously unfit for export, so are removed and eventually destroyed or used as compost. Other nuts less obviously affected are exported in spite of their high moisture and free fatty acid contents and slight mouldiness.

Of the nuts stored in Kano township in each of the two seasons 1946–47 and 1947–48, 0·22 per cent. were recorded as unfit for export. Only a small proportion of this was due to roof leaks or careless placing of rick sheets, but a single example of a leaking roof can cause a large tonnage of damage. A fairly usual site of water damage affecting a varying proportion of the nuts is the centre of the bottom layer of sacks in both pyramids and warehouses. This can affect the sack to approximately half its height, and damage has sometimes been of the order of ten tons in a 750-ton pyramid.

This basal water damage could be caused by water or water vapour rising through the concrete floor of the warehouse or the plinth of the pyramid but this did not seem very likely as the general run off of water was rapid and water did not stand round pyramids or warehouses. The high internal temperatures of groundnut stacks with a steep gradient near the ground and the drying out of the centre is evidence that some of the water damage is caused by translocation of moisture down the temperature gradient. Experiments to decide between these causes were set up by stacking parts of two stacks on waterproof tarred paper. These were finished by Mr. C. R. Hubbard

TABLE VII.

Moisture content of groundnuts brought into store in February, 1948, and free fatty acid content of the whole nuts, splits and fragments into which the samples were sorted.

Months in store	Mean R.H. %	Moisture contents %	F.F.A. %		
			Whole	Splits	Fragments
0 (Feb.) ...	18	3·1	0·3	0·3	0·8
1 (Mar.) ...	21	3·2	0·5	0·4	1·0
2 (Apr.) ...	43	3·8	1·1	2·0	6·1
3 (May) ...	53	3·9	1·6	3·9	7·2
4 (June) ...	66	4·2	2·6	6·8	10·3
5 (July) ...	73	5·3	3·2	7·4	13·5
6 (Aug.) ...	81	6·3	3·5	8·6	14·4
7 (Sept.) ...	75	4·0	3·5	9·2	16·3
9 (Nov.) ...	32	3·2	3·4	9·2	17·1
12 (Feb.) ...	18	3·1	3·5	9·8	17·2

of the Dept. of Marketing & Exports. The moisture content of nuts stored over the paper was 4·4 per cent. compared with 8·0 per cent. away from it, indicating some uptake of water or vapour through the pyramid base.

Continuous sun drying prevents water damage in outside sacks of the bottom layer.

(2) Oil losses.

The oil content of nuts does not decrease during storage, remaining in the region of 51–52 per cent. of dry weight throughout.

The dust produced by insect activity is, however, deficient in oil. Dust passing 10- and 20-mesh sieves had oil contents in the region 14–17 per cent.

Oil is not obviously pressed from nuts while stacked as it is from palm kernels. Stacking against hot walls does cause oily marks on the wall but the losses seem to be negligible.

Corby (1947) records that *Aphanus sordidus* attacked nuts stored in bulk in Yola and reduced oil content from 50 per cent. to 17·5 per cent. The Survey has not noted this bug causing the shrivelling of nuts he described, nor has it found any effect on oil content.

(3) Increase of free fatty acid.

Oil quality can conveniently be measured in terms of free fatty acid content, since fatty acids must be removed before the oil can be used as a human food. Removal of these is accompanied by removal of at least an equal quantity of good oil so that it is not economic to refine oils of high fatty acid content. These low-grade oils are directed to soap manufacture.

TABLE VIII.

Change of free fatty acid content of groundnuts after mincing.

F.F.A. % on day of mincing	F.F.A. % 23 days after mincing
7·0	13·5
7·9	15·3
6·2	12·7
13·1	25·3

(i) *due to breakage.*

A large number of estimations of the free fatty acid content (F.F.A.) of stored nuts were made. It was found that the breakage of nuts had a marked influence on the rate of increase of F.F.A. (Table VII). In a year of storage the F.F.A. of whole nuts rose to nearly 4 per cent., of splits to about 9 per cent. and of broken nuts to about 17 per cent. The F.F.A. of powdered nuts often rises to the order of 70 per cent. This phenomenon was confirmed in the laboratory by L. A. W. Hayward by mincing nuts and measuring the F.F.A. immediately, and 23 days later. In this period the F.F.A. of all samples was doubled (Table VIII). Consequently in subsequent observations on F.F.A. increase, it was usual to remove the powder and sort the samples of nuts into whole nuts, splits and fragments.

(ii) *due to moisture content.*

The effect of relative humidity and nut moisture content in accelerating the increase of F.F.A. is illustrated by Table VII which shows typical changes of F.F.A. during commercial storage in Kano. The F.F.A. content rises steeply from April to August when the humidity increases steadily, and then flattens to a steady level when the humidity falls again.

The F.F.A. of samples taken from the bottom layer of a stack was always high, varying from 5·5 per cent. to 18·1 per cent., the minimum for samples taken near the centre of this layer being 10·6 per cent. These high values are correlated with the high moisture contents of nuts in this layer.

(iii) *field observations.*

During storage, samples of nuts can only be taken from the outside of a stack and many pyramids and warehouses had to be visited during unloading to obtain samples from the middle of a stack. In general, it has proved that the F.F.A. of dust-free nuts is lowest centrally just as are the insect population and quantity of dust in similar samples. Thus in a series of samples taken through the middle of a pyramid at about four feet above ground level, the F.F.A. contents of dust free unsorted samples were 9·6, 6·6, 7·6, 9·4, 3·8, 2·5, 9·3, 7·2, 5·3, and 9·2 per cent.

All samples for F.F.A. were taken by means of a sampling spear inserted at the middle of the exposed face (usually the long side) of a sack. The average F.F.A. value obtained from 149 samples (including 38 unsorted but dust-free samples) was 5·13 per cent. Adding an allowance for the dust shipped with the nuts, it may be said that groundnuts leave Kano with an average F.F.A. of 5·3 per cent. On arrival in Britain the F.F.A. of Nigerian groundnuts, according to two of the principal oil expressing firms is about 6·5 per cent. They report a steady increase in the F.F.A. of Nigerian nuts since 1939 when the nuts arrived with an average of 3·4 per cent. F.F.A.

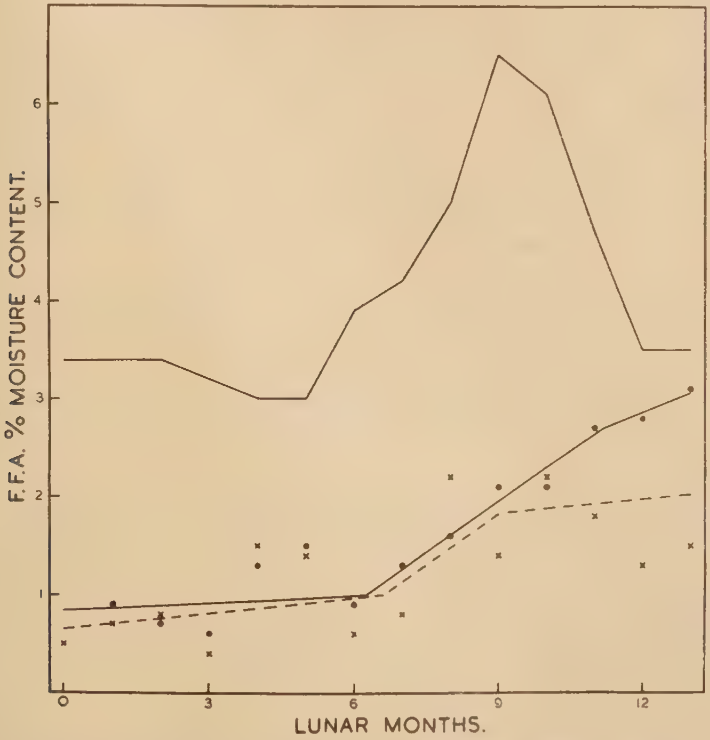

Fig. 8.—Moisture content (top line) and F.F.A. of whole nuts (broken line and crosses) and of splits plus fragments (full line and dots) stored free of insects.

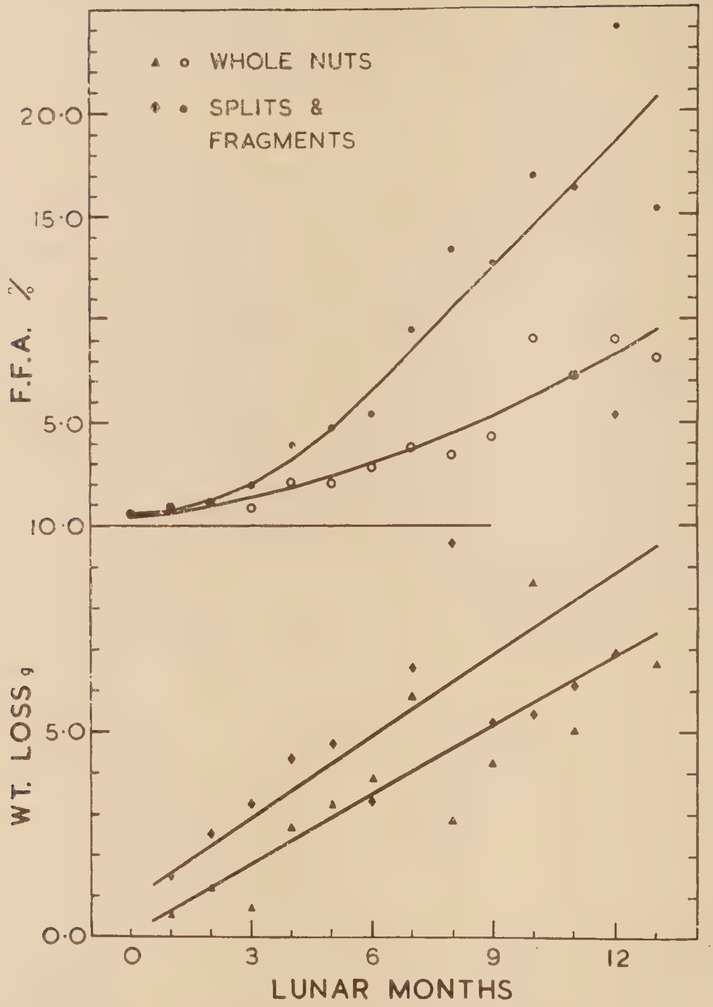

Fig. 9.—F.F.A. content and loss of weight in samples of 50 gm. of whole nuts and of splits plus fragments infested with 200 adult *Tribolium*.

(iv) *due to insects.*

Since field observations give no definite information about the effect of insects on F.F.A. increase except to show that high F.F.A. and heavy infestations occur together, a laboratory experiment was designed to show the effect of insect infestation on F.F.A. values.

The experiment was performed in a small outhouse similar in construction, temperature and humidity to an ordinary Kano warehouse and since one of the major difficulties was the keeping of controls free of unwanted insects the whole set of experimental bottles were placed in a large, tall cardboard box covered with fine wire gauze.

A sample of recently harvested, dry, insect-free groundnuts was obtained in December, 1948. This was hand-picked to separate all the whole undamaged nuts leaving a fraction consisting of splits and broken pieces in approximately equal proportions by weight. Each fraction was thoroughly mixed up and a sample taken of each for determination of F.F.A. and moisture content. Thirteen lots of each fraction of approximately 50 gm. were weighed out into Kilner jars on 9th December, and 200 adult *Tribolium castaneum*, collected from a local warehouse, were added to each of the 26 bottles. Each jar was covered with muslin fixed in position by a rubber band as also were similar jars containing insect-free nuts. The thirteen jars of each fraction were arranged arbitrarily, dated in lunar months from 6th January to 8th December 1949, and transferred to the out-building. Under the conditions of this experiment *Tribolium* does not multiply, for cannibalism restricts the development of new adults.

On reaching the date written on the label, each experimental jar was freed of insects, and dust passing through 10- and 30-mesh sieves ; the insects, living and dead, were counted and the dust and nuts weighed. These nuts and a sample from each control were analysed for F.F.A. and moisture content. Fig. 8 gives the results for moisture content and F.F.A. of controls and fig. 9 the F.F.A. and dry weight loss of the experimental samples. It will be seen (fig. 8) that even the fragments and splits reached an F.F.A. of only 3·1 per cent. after a full year's storage free of insects during which time their moisture content rose to over 6 per cent. and fell again.

Insect-attacked nuts reached 3 per cent. F.F.A in the sixth month, before the moisture content rose much, but the level of insect infestation used was much higher than occurs in normal storage. In dust-free unsorted samples, taken after six to eighteen months commercial storage, F.F.A. ranged from 1·5 per cent. to 15·5 per cent. and the average of 150 such samples was 5·3 per cent. An F.F.A. of about 3 per cent. is accepted as reasonable for groundnuts imported into Britain, so it can be seen that insects are an important agent in causing deterioration of groundnut quality. It is not clear whether the F.F.A. rise is caused by the introduction of enzymes, fungi or by the breaking down of cells but it is clearly related to the great increase in surface area caused by insects.

A similar experiment was carried out with broken nuts but using moths. A mixture of adult *Plodia interpunctella* and *Ephestia cautella* were added to weighed amounts of nuts and the experiment ended ten weeks later when the next generation was beginning to emerge. No appreciable increase of F.F.A. over the controls was noted in this period.

During 1950, experiments were performed at the Pest Infestation Laboratory to evaluate the effect of *Trogoderma* on F.F.A. The experiments were carried out with whole nuts at 33°C. and two relative humidities, 30 per cent. and 70 per cent. Sixty-gramme samples of nuts were infested with 250 freshly hatched larvae which were replaced every five weeks by a similar batch of newly hatched larvae. It became progressively difficult to remove the old larvae which tunnelled into the nuts and consequently the infesting populations increased somewhat during the experiment.

One sample of nuts from each humidity was removed for estimation of weight loss and measurement of F.F.A. and moisture content every two and a half weeks. Nuts at both humidities were badly damaged, the weight loss reaching about 20 per cent. in six months at 30 per cent. R.H. and 40 per cent. at 70 per cent. R.H. The moisture content of the experimental nuts (estimated by drying at 102°C. for three hours) at 30 per cent. R.H. was 4·0 per cent. and at 70 per cent. R.H., 6·5 per cent. There was no great difference in F.F.A. between samples from the two humidities in 20 weeks, by which time the F.F.A. had reached 5 per cent.

During the last five weeks of the experiment the nuts at 70 per cent. R.H. became very moist (over 10 per cent.) and mouldy with an F.F.A. of 25 per cent. The results are plotted in fig. 10. *Trogoderma* attack, like *Tribolium* infestation, is obviously capable of raising the F.F.A. of groundnuts.

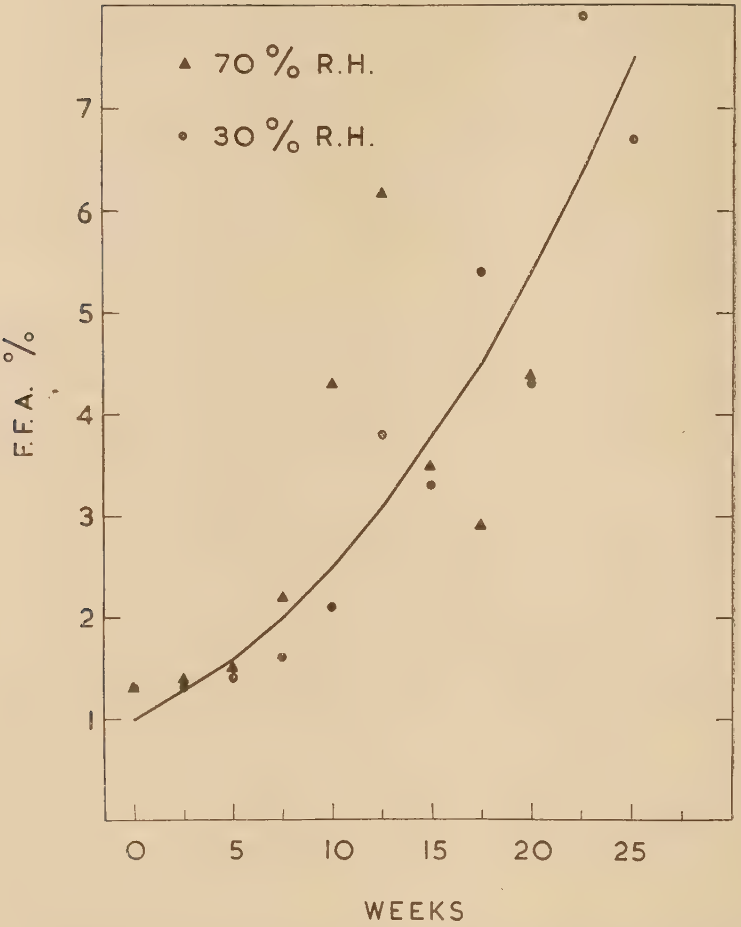

Fig. 10.—Increase in F.F.A. content of whole groundnuts stored at 30 per cent. and 70 per cent. R.H. with 250 *Trogoderma* larvae per 60 gm. sample. The line fitted represents the results at 30 per cent. R.H.

(4) Effect of powdered nuts on quality.

In addition to the obvious effect of increasing the F.F.A. content, the presence in a commercial sample of nuts of large amounts of powder lowers the quality of the refined deodorised oil by giving it a dark colour, a bitter flavour and poor keeping quality.

The oil obtained from the testa of groundnuts is also very dark and has a high F.F.A. content.

Monetary losses.

The financial losses caused by prolonged storage are difficult to estimate but a number of items can be given. First there is the direct weight loss of about 5 per cent. due to insects and water damage, which is real, even though apparently cancelled out by water uptake. There is the loss due to quality depreciation. Since the F.F.A. rises some 6 per cent. during storage, some 12 per cent., at least, of the edible oil is diverted to soap making.

The emergence of *Trogoderma* as a significant pest has introduced a new source of loss in the form of damage to sacks. Replacement of sacks has also been necessary owing to the water damage, affecting the bottom layer of all stacks. As the yearly cost of this is in the order of £25,000 it would seem well worth while to introduce some form of dunnage to prevent or reduce this damage. In 1947–48 the cost of replacing sacks damaged by *Trogoderma* was over £7,000 and in the following season was probably double that figure. Major damage of this kind can be avoided by treating infested lots before the population increases.

Treatment of infested stock has introduced extra expenses. Those directed at preventing the build-up of insect population can be regarded as normal storage expenditure, but they must be accompanied by common sense storage hygiene. So far, much *Trogoderma* spread has been caused by carelessness and the amount of fumigation needed has been unnecessarily increased. Costs of labour and handling for fumigation have been three shillings per ton and of gas about one shilling per ton. New methods of fumigation are under consideration to avoid the transport costs, and it is hoped they will also reduce insect infestation to levels at which the primitive storage hygiene will be unimportant.

Summary.

In Nigeria, shelled groundnuts are stored in sacks in covered warehouses and as pyramids in the open air. At the beginning of storage the nuts comprise approximately equal quantities of whole, split and broken nuts of a moisture content of 3·4 per cent. The sacks are exposed to direct hot sun whilst stacking.

The mean monthly maximum shade temperature in Kano ranges from 101°F. in April to 85°F. in January and August and the mean monthly minimum from 75°F. in May to 56°F. in January. Monthly maximum relative humidities range from 100 per cent. in August and September to 45 per cent. in February, and the monthly minimum from 71 per cent. in August to 12 per cent. in February. The range of mean relative humidity is 81 per cent. in August and 18 per cent. in February. Rains fall between April and September, 70 per cent. falling in July and August. Heavy falls are recorded on about 25 days.

Inside warehouses, the maximum monthly temperatures are 102°F. in May and 79°F. in January and February, and minimum temperatures are 81°F. in June, and 58°F. in February. In August the mean relative humidity range is 93 per cent. to 70 per cent. In December it is 34 per cent. to 20 per cent.

Just under the roof of a warehouse and on the surface of pyramids the diurnal range is very large.

Thermocouples built into stacks showed that initial stacking temperatures in 1948–49 were about 104°F. (40°C.). If *Trogoderma* were present this temperature was maintained and even increased to about 113°F. (45°C.) but in its absence the temperature of the stack fell slowly during the wet season and more rapidly after September to 80°F. (27°C.) approximately in February.

The moisture content of small samples and the surface nuts of stacks falls to 3·0 per cent. in April rises to 6·5 per cent. in August and falls back to 3·3 per cent. by January. The hot core of stacks causes drying out of the centre of stacks so that nuts have been found as dry as 2·3 per cent. The bottom layer stacked against the comparatively cool ground becomes wet, probably by translocation of moisture and is damaged. Sound nuts sampled in this layer have shown 6 per cent. moisture.

The more equable temperature and humidity conditions and a permanent low light intensity make warehouses a favourable environment for insects. The large and violent changes at the surface of pyramids render them unsuitable for insect

multiplication. The internal stack temperatures are too high for all insects except *Trogoderma*.

A list of the insect pests associated with stored produce in Kano, northern Nigeria, is given. This includes as major pests of groundnuts, *Tribolium castaneum*, *Trogoderma granarium*, *Ephestia cautella* and *Plodia interpunctella* ; major pests specific to grain included *Calandra oryzae*, *Rhizopertha dominica* and *Sitotroga cerealella* and specific to hides, *Dermestes maculatus*. Insect species which were numerous locally in patches were *Alphitobius laevigatus*, *Palorus ratzeburgi*, *Caryedon fuscus*, *Laemophloeus ferrugineus*, *Oryzaephilus mercator*, *Mesostenopa picea*, *Thorictodes heydeni*, *Corcyra cephalonica*, *Aphanus sordidus*, *Lyctocoris campestris* and *Thermobia* sp.

Species widespread in small numbers were *Tribolium confusum*, *T. anaphe*, *Anthicus floralis*, *Phradonoma tricolor*, *Attagenus gloriosae* and *Tenebroides mauritanicus*.

A number of species is found in Lagos but not in Kano. These include *Araecerus fasciculatus*, *Ahasverus advena*, *Gibbium psylloides*, *Dermestes ater*, *Thaneroclerus buqueti* and *Necrobia rufipes*. All these need high humidities.

Interesting absentees from Nigeria are *Ephestia elutella* and *E. kuehniella*, *Hofmannophila* and *Endrosis*, *Gnathocerus*, *Latheticus*, *Trogoderma versicolor*, *Stegobium paniceum*, and *Ptinus tectus*. Most of these cannot tolerate the high temperature.

Insect activity is very marked out of doors at dusk and all day inside dark warehouses. The time and extent of peak out-door activity is variable and its relation to the weather not clear. No successful method of estimating numbers was devised. Sampling groundnuts with a sack sampler was unsuccessful but counting numbers on selected wall areas and trapping in plates of water are both promising but laborious.

The special problem of *Trogoderma* infestation is discussed. The adult of this beetle cannot fly, but, even so, it has spread rapidly since it was first discovered. It is concluded that it is an endemic insect whose habits made its presence unsuspected until it became sufficiently numerous to be an economic pest in Kano. It is shown that it affected stored groundnuts in Kano in 1946, and probably in 1944. Build-up in Kano is attributed to long undisturbed storage by agents, which may receive a small initial impetus by a period of storage before sale to agents by middlemen. Cross infestation inside Kano occurred on a large scale in 1949, and many warehouses are now infested and should not be used in future for food storage.

There is some risk that carriage of untreated groundnuts to ports might establish *Trogoderma* there, but competition with *Tribolium* and predation by *Lyctocoris* make it unlikely to succeed in the cooler, damper regions.

A sampling trial was done with the standard conical spear sampler used by Nigerian Produce Examiners. It was found that the sampling process breaks about 4 per cent. of whole nuts present at the sampling points, and that the sampler contains less whole nuts, approximately 5 per cent. of the number originally present, than are present at the sampling point.

Nuts tend to segregate so that whole nuts come to the top of the sack and dust and small pieces filter to the bottom. The middle of the sack contains a representative mixture of nut fractions, but only about half to three-quarters of the mean amount of dust present in the whole sack. The percentages of whole nuts and dust in a sample taken with a spear sampler at the middle of an exposed sack face should be increased by one tenth and one half, respectively.

Weight changes of stored groundnuts are due mainly to moisture uptake and insect attack. If groundnuts are removed at a steady rate throughout the year, the average increase in moisture content for a year's storage is about 1 per cent. The picture is complicated because the high temperatures experienced inside stacks causes central drying with an increase in moisture content of the base of stacks.

Average overall loss due to insect attack is about 4·5 per cent., of this about 2 per cent. is in the gross weight of sacks after adjustment for change of moisture content and about 2·5 per cent. is insect frass remaining inside the sacks. Losses are greater in warehouses than in pyramids, in outer sacks than in inner ones and in the presence of *Trogoderma*.

These losses pass unnoticed in practice because the dust is retained in the sacks and the 2 per cent. weight loss is compensated by the 1 per cent. gain due to moisture uptake in Kano and a further similar gain in transit and at port.

Termites do some damage by eating sacking and causing spillage of nuts and hedgehogs may eat some nuts.

The quality damage caused by water is so obvious that affected nuts are discarded; about 0·25 per cent. are thus damaged each season. This type of damage is mainly confined to the base of stacks and is partly due to translocated moisture. Oil losses are negligible but oil quality as measured by free fatty acid content (F.F.A.) deteriorates during storage. F.F.A. increases most in small pieces of nuts and least in whole nuts. High moisture content accelerates the rate of F.F.A. increase and so does insect attack.

In field conditions the highest F.F.A. values are observed peripherally and at the base of stacks. The average F.F.A. of nuts leaving Kano in a year was 5·3 per cent. and of Nigerian nuts arriving in Britain 6·5 per cent.

Powdered nuts spoil the quality of refined oils.

Monetary losses are incurred as a result of weight losses due to insects and water damage, to refining costs resulting from increased F.F.A., to the destruction of sacks by water and *Trogoderma* infestation and to extra treatment costs made necessary by the excessive spread of pests.

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THE INSECTS ASSOCIATED WITH EXPORT PRODUCE IN SOUTHERN NIGERIA.

By G. S. Cotterell.

Food commodities stored in southern Nigeria are liable to infestation not only by native insects but also to cross infestation from export produce in transit from the north of the country. There is also some possibility at the ports of the introduction of insects on imports.

In the ports endemic insects such as *Necrobia rufipes* (Deg.) and *Ahasverus advena* (Waltl) spread to groundnuts awaiting shipments, and conversely groundnut pests such as *Plodia interpunctella* (Hb.), *Corcyra cephalonica* (Staint.) and particularly *Tribolium castaneum* (Hbst.) spread to cocoa and palm kernels produced in the south.

The population of *Ephestia cautella* (Wlk.) infesting both cocoa and palm kernels is further augmented by the individuals introduced on groundnuts. Much of this spread is caused by using old groundnut sacks for transporting palm kernels. Because of the shortage of jute sacks, a considerable proportion of groundnuts has been shipped in bulk, the bags being slit on being loaded on to ship and skipped into the hold. The empty sacks are then taken to repair depots at the ports of Apapa and Port Harcourt and finally distributed to palm kernel marketing centres. These sacks carry an infestation of *Ephestia* living on groundnut dust lodged in the interstices, as well as of *Tribolium* and other insects infesting groundnuts. Not only are these sacks used for the conveyance of palm kernels but some find their way to farmers and brokers who use them as service sacks for the marketing of cocoa and other food commodities. A small fumigation plant for the treatment of used sacks has been designed and is already in operation at Lagos.

Cocoa Beans.

The insects of major importance in southern Nigeria are *Ephestia cautella*, known as the West African Cocoa Moth, *Lasioderma serricorne* (F.), the Tobacco Beetle, and *Araecerus fasciculatus* (Deg.), the West African Cocoa Weevil. Others are either scavengers, feeders on mould affecting produce, or parasites or predators of the above insects.

Ephestia cautella is a major pest of stored cocoa beans in all West African territories where cocoa is produced for export, and is common in all stages of cocoa storage and at all seasons of the year, becoming abundant when storage is prolonged. Adults of this species are frequently abundant in cocoa stores in Nigeria early in the main crop season, October, whereas in the Gold Coast incidence usually only becomes noticeable towards the end of the marketing season. This is largely due to the storage of palm kernels in the same or adjacent premises in Nigeria whereas in the Gold Coast there is little storage of palm kernels.

Infestation originates in the farmers' and brokers' storage premises, which are generally small, rarely cleaned, and may contain small parcels of beans which are below standard and which owners are reluctant to dispose of if they can be marketed later by mixing with a following crop in order to conform to an exportable grade.

Damage is caused by the larvae which move from bean to bean during the course of their development. Females lay eggs two days after emergence and one female is capable of producing 250 eggs all of which are laid within two days of emergence of the adult. Eggs are laid indiscriminately over the surface of bagged cocoa. Larvae can only gain access to the cotyledons if the testa is broken. The ovipositor holes made by the female *Araecerus* during the course of oviposition are sufficiently large to permit entry of newly hatched *Ephestia* larvae and germinated beans, and beans broken by handling, can be entered by larvae at all stages of development. Larval development can be completed on mucilage adhering to the testa and a number complete their development in this way. Development can also be completed in undisturbed dust in stores and in dust retained in the interstices of empty sacks. Pupation takes place on the surface of bags, in the angles between resting bags and occasionally in the beans themselves, provided they are near the surface. Occasionally larvae may migrate a short distance to pupate in wall crevices. This may happen when beans are bulked on the floor for grading purposes, disturbance having the effect of stimulating larvae to leave the heap, but there is no general migration as there is with *Ephestia elutella* in temperate climates.

The life-cycle averages 65 days under normal conditions. Development carries on throughout the year provided food material is available. Incidence is greatest in the peripheral layers of bags in a stack. Adults are active at dusk flying from store to store.

The Braconid, *Bracon* (*Microbracon*) *hebetor* Say, is an ectoparasite of the larva but is an ineffective control except in heavy infestations.

Lasioderma serricorne is a pest of stored cocoa of primary importance only in Nigeria where it was first recognised in 1930. Prior to this it had been recorded in the Gold Coast as a pest of secondary importance confined to sweepings. In Nigeria, since this date, incidence has steadily increased and it is now regarded as a major pest and one of the chief causes of the down-grading of cocoa. In some instances attack has reached alarming proportions following prolonged storage due to delays in evacuation to port.

Thoroughly dry beans are as prone to attack as those that are not commercially dry. In Nigeria *Lasioderma* is a serious pest of the stored tobacco leaf used in a large local cigarette factory at Ibadan where it attacks both locally grown and imported American and East African tobacco leaf. Some doubt has been expressed as to whether or not the pest originated from imported tobacco. The insect can be an important pest of starched book-bindings in the Gold Coast, the attack dating from the importation of infested books from Ceylon in 1924.

Primary infestation takes place in the farmers' and brokers' storage premises and, as with *Ephestia*, the storage of small quantities of below-standard beans in these premises forms a primary source of infestation of fresh stocks. Re-infestation continues in all storage phases. Larvae feed on the cotyledons and pupation takes place inside the bean, the adult beetles eating their way out. In an active infestation at least three beans are infested to every one showing an exit hole. Adults are active at dusk and fly out from stores.

The following notes on *Lasioderma* infestation have been obtained from the Produce Inspection Division of the Department of Marketing and Exports, supplemented from records obtained from the Agricultural Entomologist, Department of Agriculture.

1930—First recorded in Nigeria in a bag of cocoa beans which had been kept for one year in Entomologist's laboratory, Ibadan, Western Provinces.

1933—In African owned premises, Ibadan, in poor quality cocoa beans which had been in store for some time. (First record in cocoa stores.)

1935—In sample beans sent to British Association of Research for the Chocolate etc. Trades (Nicol 1935).

1940—Recorded at Ijebu-Ode, Ondo Province, in light crop cocoa.

1942—Agege, Lagos Colony, in light crop cocoa.

1946—Many centres in Ondo Province, and at Agbabu, a creek port for Ondo Province evacuating by lighter to Lagos.

Since then it has been recorded annually in cocoa stores generally in the western provinces of Nigeria. The 1946 infestation in Ondo Province was severe and has been attributed to the slow evacuation of cocoa from that area via the creek ports.

Testing a bag of cocoa for *Lasioderma* infestation with a bag sampler has proved unsatisfactory. It has been found that the best method is to open the top of a bag and " snake " the beans along the floor. By this method whole beans come out first, the final lot consisting of dust, broken beans, and adult beetles.

Examination of a heavily infested stack has given the following figures :—

Outside bags—3·5 per cent. infested (beans with exit holes).

Second and third rows—8 per cent. infested.

The cocoa had been in store for eight months and infestation had come from the centre of the stack.

Araecerus fasciculatus is dependent on a high moisture content of cocoa beans for development. Primary infestation occurs during the drying process in the open, adult females being attracted to beans of between 20 and 12 per cent. moisture content, secondary infestation taking place in all subsequent storage premises provided beans are not commercially dry. The mature female pierces the testa with its ovipositor and this may be done many times before depositing an egg below the surface, each hole being sufficiently large to permit of the entry of a newly hatched *Ephestia* larva. Pupation takes place inside the bean. The cycle from egg to adult varies from 47 to 135 days in the laboratory depending on moisture content of the bean and is completed in one bean. At 8 per cent. and below, development is not completed. Life-history details have been published by Cotterell (1934). Incidence is greatest in the peripheral bag layers of a stack.

With better attention to drying, infestation has been considerably reduced except in areas where thorough drying is difficult.

Araecerus attacks coffee berries, maize and cassava (*Manihot*) flour in West Africa, and also breeds in the seed pods of numerous leguminous " bush " plants.

Losses in cocoa are mainly due to attack by *Ephestia* and *Lasioderma*. No attempt has been made to assess losses due entirely to insect infestation. Weight loss is negligible and loss is more one of quality than of any other. Cocoa beans are re-inspected and re-graded if necessary, at intervals during storage and on arrival at port. Despite regular shipments and reasonably short storage, down-grading figures in the season 1948–49 obtained from the Department of Marketing and Exports have been of the following order :—

29,000 tons	Grade I	to Grade II.
10,000 tons	Grade I	to No Grade.
15,000 tons	Grade II	to No Grade.
640 tons	Grade III	to No Grade.

At current prices, the financial losses resulting from the down-grading are considerable.

Slatey beans are caused by insufficient fermentation, germination resulting from the harvesting of over-ripe pods or over-fermentation, and with flat and otherwise defective beans ; these factors remain constant during storage. Dade (1929) has shown that mould does not continue to develop under 8 per cent. moisture content. Theoretically therefore losses should be entirely due to insects. Storage conditions in the south, however, do not always permit of the moisture content of cocoa beans remaining below 8 per cent. on account of their hygroscopic character (Scott, 1929), and some parcels of cocoa may be marketed which are not commercially dry. Sample bags of cocoa stored in one of the Survey's experimental sheds at Lagos (Apapa) over a period of six months slowly deteriorated due to increase in insect infestation and incidence of moulds although the moisture content remained in the vicinity of 8 per cent. or below.

The important factor affecting the trade is the presence of live insects in consignments arriving at the manufacturers' premises in the United Kingdom, and the danger of cross-infestation to the manufactured product. In this respect infestation by *Ephestia* is important ; neither *Lasioderma* or *Araecerus* can continue to develop under temperate storage conditions.

Palm Kernels.

Ephestia cautella is the chief infesting insect and appears to develop more readily in this commodity than in cocoa, feeding almost entirely on broken kernels and on the surface of kernels. A considerable amount of cross-infestation occurs in localities where these two commodities are marketed and stored together.

Other insects infesting palm kernels are *Necrobia rufipes*, *Carpophilus dimidiatus* (F.), and *Oryzaephilus mercator* (Fauv.). *Carpophilus* is common in cracked kernels and is associated with the presence of mould. *Pachymerus* (*Caryedon*) *lacerdae* (Chevr.) is occasionally found in kernels marketed in the eastern provinces, primary infestation taking place in the field before the kernels are harvested. The insects associated with palm kernels, with the exception of *Ephestia*, are more common in the eastern provinces than in the western, presumably due to poorer methods of preparation for market and in some cases to lack of facilities for quick evacuation.

Losses caused by insect infestation appear to be negligible, mould being the chief deterioration factor.

Other Export Commodities in Transit.

Tribolium, *Ephestia* and *Plodia* continue to develop rapidly in groundnuts whilst in transit storage, but in *Trogoderma granarium* Everts development appears to be retarded.

Aphanus sordidus (F.) is of frequent occurrence on bagged groundnuts and benniseed at the ports of Warri and Burutu at the mouth of the Niger in transit storage premises.

Capsicums for export are frequently infested by *Tribolium* on account of cross-infestation during transit and at the port. This may have a serious effect on their marketable value, particularly in the American market.

Local Control Measures.

Routine control measures have in the past been confined to store hygiene and the trapping of adult moths and beetles in cocoa stores. Considerable attention has been given to the drying of cocoa beans with a consequent diminution in the number of beans attacked by *Araecerus* at marketing.

Store hygiene includes the lime-washing of storage premises at least once a year which, although lime-wash is not insecticidal, insures that stores are reasonably cleaned. Whilst cleaning is regularly carried out in merchants' up-country storage premises, it is less frequently done in port transit premises owing to the continuous congestion of produce.

Trapping.

Trapping of adult insects with "Ate" strands is a routine measure in up-country premises. The dried mid-ribs of oil palm leaves are slung vertically from strings surrounding cocoa stacks, each rib having previously been coated with a mixture of wild rubber latex, coagulated with lime juice, and shea butter or palm oil to give the required consistency (Golding, 1941). The method was originally adopted for the control of *Ephestia* and takes advantage of the tendency for adult moths of this species to settle on strings. Adult beetles of *Lasioderma* are similarly attracted and caught but it is doubtful if much control of either species is effected.

Traps containing weak soap solutions placed in shallow pans on the floors of storage premises are also used but captures are negligible in proportion to the insect population in stores. This method was used to compare the abundance of the various species in a typical store. Recording was commenced by R. W. Howe, Senior Control Entomologist, during a visit to Lagos and was continued by H. M. B. Somade, Control Chemist. These weak solutions of soap in water having been found by experience to attract adults of most of the pest species infesting cocoa beans, a number of dishes 10 ins. in diameter and 1½ ins. high were placed round a stack of bagged cocoa, in a typical store in Lagos, spaced at intervals of 6 ft. Each was filled with 200 mls. of solution made by dissolving 24 grammes of locally made carbolic soap in 500 mls. of water and then diluting to 2,400 mls.

Periodically the dishes were collected and the solution, which in most cases had become partly gelled, was strained through fine mesh wire gauze. The insects found were washed with water and classified according to species. The results are given in Table I.

Captures of female *Ephestia cautella* exceed those of males and they were all fertilised. The relative humidity during the period was never less than 78 per cent. and on two occasions in September it was 98 per cent. The presence of traps caused no apparent diminution in the insect population. The store was provided with large ventilation spaces at the tops of the walls and insects were able to fly in and out, and did so particularly at dusk when insect activity is high.

TABLE I.

Numbers of insects caught in plates of soap solution placed in a Lagos cocoa palm-kernel store on eight days during September and October 1949.

	Total caught in 8 days	Range of catch per day	Geometric mean *
Necrobia ...	905	71–158	111
Lasioderma ...	453	26–145	49
Ephestia ♀ ...	258	6– 75	23
,, ♂ ...	81	3– 25	9
,, both sexes ...	339	9–100	31
Ahasverus ...	298	13– 94	32
Hemiptera ...	226	4– 52	21
Araecerus ...	101	3– 59	7
Carpophilus ...	40	1– 21	3
Laemophloeus ...	27	0– 7	3
Tribolium ...	16	0– 9	1
Parasites ...	11	0– 2	1

*Found from mean log.

The Table is of value as a record of flying insects found in a typical cocoa and palm-kernel transit store, but records are required over a much longer period to enable conclusions to be drawn regarding periodic fluctuations in insect populations.

List of Insects affecting Produce in southern Nigeria.

The following list was compiled by Mr. K. G. Smith, Control Entomologist. The species recorded were found in port transit stores in Lagos on export produce, cocoa, C ; palm kernels, PK ; groundnuts, G ; cotton seed, CS ; shea nuts, S ; capsicums, CP ; and benniseed, B ; and in local storage premises on local foodstuffs, maize and maize products, M ; rice, R ; and cassava meal, CM.

Family	Species	Produce infested								
HEMIPTERA										
Anthocoridae	*Lyctocoris campestris* (F.)	C							R	
Lygaeidae	*Aphanus sordidus* (F.)									B
HYMENOPTERA										
Bethylidae	*Cephalonomia tarsalis* (Ashm.)	C								
,,	*Holepyris hawaiiensis* (Ashm.)	C		G						
,,	*Plastanoxus munroi* Richards	C								
,,	*Rhabdepyris zeae* Turn. & Wtstn.	C								
Braconidae	*Bracon* (*Microbracon*) *hebetor* Say	C		G						
Chalcidae	*Antrocephalus mahensis* Masi	C								
COLEOPTERA										
Anobiidae	*Lasioderma serricorne* (F.)	C								
Anthicidae	*Anthicus floralis* (L.)	C								
Anthribidae	*Araecerus fasciculatus* (Deg.)	C				S				
Bostrychidae	*Dinoderus minutus* (F.)									CM
,,	*Rhizopertha dominica* (F.)							M		
Bruchidae	*Caryedon fuscus* (Goeze)			G						
Cleridae	*Necrobia rufipes* (Deg.)		PK	G	CS					
,,	*Thaneroclerus buqueti* (Lef.)	C								CM
Cucujidae	*Ahasverus advena* (Waltl)	C		G						
,,	*Laemophloeus ferrugineus* (Steph.)	C		G	CS			M		
,,	*Oryzaephilus mercator* (Fauv.)		PK	G		S		M		
,,	*O. surinamensis* (L.)								R	
Curculionidae	*Calandra oryzae* (L.)							M	R	
Dermestidae	*Attagenus gloriosae* (F.)			G						
,,	*Dermestes ater* Deg.			G						
,,	*Orphinus aethiops* Arrow			G						
,,	*Trinodes hirtus* (F.)			G						
,,	*Trogoderma granarium* Everts			G						
Histeridae	*Carcinops quattuordecimstriata* (Steph.)			G						
Mycetophagidae	*Typhaea stercorea* (L.)			G				M		
Nitidulidae	*Carpophilus dimidiatus* (F.)	C	PK	G						
,,	*C. hemipterus* (L.)		PK					M		
,,	*C. minutus* (L.)			G						
Ptinidae	*Gibbium psylloides* (Czenp.)	C								
Tenebrionidae	*Alphitobius laevigatus* (F.)			G	CS					
,,	*Palorus ratzeburgi* (Wissm.)			G				M		CM
,,	*Tribolium castaneum* (Hbst.)	C	PK	G	CS	S	C	M	R	CM
Trogositidae	*Tenebroides mauretanicus* (L.)		PK	G	CS		CP	M	R	
LEPIDOPTERA										
Galleriidae	*Corcyra cephalonica* (Staint.)	C		G				M	R	
Gelechiidae	*Sitotroga cerealella* (Ol.)							M		
Phycitidae	*Ephestia cautella* (Wlk.)	C	PK	G	CS	S	CP	M		CM
,,	*Plodia interpunctella* (Hb.)	C		G				M		
Pyralidae	*Pyralis manihotalis* Gn.			G						CM
Tinaeidae	*Tinaea fuscipunctella* Haw.			G						

Summary.

The problem of insect infestation of stored export food commodities in southern Nigeria is discussed, and a list of insects is given. At the ports there is considerable cross-infestation between commodities produced in northern and southern Nigeria awaiting shipment.

Old sacks used for the storage and transit of groundnuts are responsible for the spread of insects to palm kernel and cocoa marketing centres in the south. After bulk shipments of a portion of the groundnut crop, sacks are repaired and distributed for the shipment of palm kernels and some of them may be used by farmers and brokers as service bags for the marketing of cocoa and local food commodities. The importance of disinfestation before distribution is realised, and a small fumigation plant is in operation at port.

Ephestia cautella and *Lasioderma serricorne* are the major pests of stored cocoa beans. Both originate in farmers' and brokers' stores which are rarely cleaned, and in which small parcels of low-grade beans may be retained for mixing with a following crop to conform with an exportable grade. *Ephestia cautella* also infests palm kernels, and the early abundance of adult moths in cocoa stores up country during the marketing season is considered to be largely due to the storage of palm kernels in the vicinity. The development of *Ephestia* larvae can be completed on the outside of cocoa beans, only germinated or damaged beans being penetrated.

The infestation of cocoa beans by *Lasioderma* is of primary importance only in Nigeria. It was first recorded as attacking cocoa beans in 1930 and since then the incidence has steadily increased. Attack becomes serious if storage is prolonged and thoroughly dry beans are readily attacked. *Lasioderma* is a serious pest of stored tobacco leaf in southern Nigeria, both locally grown and imported leaf being attacked. Adult beetles are active at dusk.

The Anthribid, *Araecerus fasciculatus*, has decreased in importance as a pest of cocoa. Infestation originates during sun drying, a moisture content of between 20 per cent. and 12 per cent. being favoured by ovipositing females, but secondary infestation takes place in subsequent stages of storage if the beans are not commercially dry. Larval development is not completed in beans of 8 per cent. moisture content or under. With better drying, seasonal infestation has been considerably reduced. Attack by adult beetles prepares the way for subsequent *Ephestia* attack by damaging the testas.

Losses in cocoa are almost entirely due to *Ephestia* and *Lasioderma* and chiefly affect quality. Infestation may result in a considerable tonnage being down-graded between marketing and shipment. Infested consignments arriving at the manufacturers' premises are an important factor because of the danger of cross-infestation to the manufactured product.

Insects associated with palm kernel storage are *Ephestia cautella*, *Necrobia rufipes*, *Carpophilus dimidiatus*, and *Oryzaephilus mercator*. Losses caused are at present negligible, mould being the main deterioration factor.

Tribolium castaneum, *Trogoderma granarium*, and *Plodia interpunctella* continue to develop on groundnuts whilst in transit storage at port. *Trogoderma* development is retarded and this has been made the subject of a separate study.

Local routine control measures are discussed. These consist mainly of attention to storage hygiene, and the trapping of adult moths by the use of "Ate" strands.

A comparison of the abundance of various species in a typical cocoa store has been made by trapping in weak soap solutions placed out in shallow pans, and results are tabulated.

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STUDIES ON BEETLES OF THE FAMILY PTINIDAE.
VII.—THE BIOLOGY OF FIVE PTINID SPECIES FOUND IN STORED PRODUCTS.

By R. W. Howe and H. D. Burges.

(Plates VI and VII.)

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The work described in this paper on five species of Ptinid beetles was carried out at the same time as more detailed work on *Ptinus tectus* Boield. This species was first found in Britain only about 60 years ago (Chitty, 1904) but it spread very rapidly and has been a serious and widespread pest for at least twenty years. The object of the experiments described here is to find reasons why other established species, *Niptus hololeucus* (Fald.), *Gibbium psylloides* (Czenp.) and *Trigonogenius globulus* Sol., remain comparatively unimportant, and to assess the likelihood of the two newly introduced species, *Stethomezium squamosum* Hinton and *Eurostus hilleri* (Reitt.), becoming pests in the future.

Occurrence and Distribution.

Hayhurst (1940) and Hinton (1941) list the very wide range of foodstuffs and other produce on which the Ptinids investigated here, particularly *G. psylloides* and *N. hololeucus*, have been found. The beetles are unlikely to have been breeding on many of the substances mentioned.

G. psylloides, the hump beetle (Pls. VI, *a* & VII) is a cosmopolitan species but is found more frequently in hot climates and less frequently in Britain than either *T. globulus* or *N. hololeucus*. O'Farrell and Butler (1948) report that it is rare in Northern Ireland. It has been found in all types of building in which food is stored. Curran (1946) reports that " very rarely it occurs in large numbers on seaweed used for insulation ". Stebbing (1914) reports *Gibbium* sp. from under the bark of teak-wood, which may be a natural habitat. *G. psylloides* has probably been long associated with man as it has been found in ancient Egyptian tombs by Alfieri (1931).

The golden spider beetle, *N. hololeucus* (Pl. VI, *b* & Pl. VII) is the most common of the five species dealt with in this paper. It sometimes occurs in considerable numbers and is described by Hayhurst (1937) as an " important pest " in railway premises. The distribution of this species is cosmopolitan in temperate climates, but it is not found in the tropics. It occurs in houses and most types of storage place, being described by O'Farrell and Butler (1948) as " more essentially a warehouse scavenger than *P. tectus* ". After a report that it damaged structural timber in Germany a number of authors (*e.g.* van Emden, 1928 ; Marcus, 1930) established that it did not feed on wood.

The nests of bees, wasps and birds provide a natural habitat for *N. hololeucus*. Tuck (1897) found it in nests of *Dolichovespula* sp. and Lloyd (1945) has reported adult beetles in nests of the jackdaw. G. E. Woodroffe and B. J. Southgate of this laboratory have made the following records of the occurrence of this species :—in blackbird and sparrow nests in Regent's Park, London ; in sparrow nests at a private house at Upton Grey, near Basingstoke, Hants ; and in pigeon nests in public buildings at Chelmsford, Essex and S. Kensington, London, during the autumn of 1950 : also in pigeon nests at Bristol in the spring of 1951.

T. globulus (Pls. VI, *c* & VII) is cosmopolitan, but is less common than *N. hololeucus* and generally occurs in small numbers only. It was originally described from Chile and was first recorded in Britain in 1900 by Tomlin (1900). It is now found in houses and all kinds of storage places. Woodroffe and Southgate have recorded this species from pigeon nests in London buildings at Peckham Rye, Charing Cross and the Strand during the autumn of 1950 and again from pigeon nests at Bristol in the spring of 1951.

E. hilleri (Pls. VI, *d* & VII) is a Japanese species first found in this country in 1939 (Howe, 1940), which soon spread to widely separated areas in granaries and warehouses (Donisthorpe, 1941 ; Hinton, 1941) but was rapidly brought under control. At the present time it is found infrequently in this country. It is " well established " in warehouses and storage places in Northern Ireland (O'Farrell & Butler, 1948), although rare in comparison with other Ptinid species. Zacher (1939) found it in large numbers in a Hamburg granary in 1935. It is also found in Japan and Canada.

S. squamosum (Pls. VI, *e* & VII) was first described (Hinton, 1943) from beetles infesting plant specimens at the Imperial Institute. These plants had been brought from S. Africa and Egypt about twenty-five years previously. In 1944 specimens were sent for identification from S. Africa (Potchefstroom) by Dr. M. J. Oosthuizen (Howe, 1949a). It has not been found in British warehouses.

Damage.

Unless an infestation is very heavy, comparatively little food is eaten by Ptinids and damage by the production of frass is not obvious. Much damage to the saleable value of high grade food is caused by soiling with silk and cocoons. Larvae may pupate between or upon the layers of paper or cardboard used in packing so that, when the packets are opened, the insects are quickly noticed, however few may be present. The larvae, during their search for pupation sites, frequently leave the food on which they have developed, boring through the paper, cardboard, or sacking of containers. Much damage is done in this way. *P. tectus* and *P. fur* are known to damage wooden containers in this manner (Shapiro, 1948).

Natural Enemies.

No insect parasites of Ptinids were encountered in the laboratory. Van Emden (1931) records that the Bethylid, *Cephalonomia quadridentata* Duchaussoy, accepted *N. hololeucus* as a host in experiments, and Cotton and Good (1937) record *C. nigricornis* Sarra as parasitising *N. hololeucus.* The same authors record the Clerid, *Corynetes coeruleus* (Deg.), as a Ptinid predator.

The mite, *Pediculoides ventricosus* (Newp.), was found on larvae and adults of *G. psylloides* at 25°C. and 70 per cent. R.H. in January, 1949. This species can also attack other Ptinids. *Cheyletus eruditus* (Schr.) has been found in cultures of all species and *Typhlodromus tineivorus* Oudm. has been found in cultures of *S. squamosum.* The non-predatory species, *Glycyphagus domesticus* (Deg.) and *G. destructor* (Schr.), have also been found in cultures. Hickin (1941b) has recorded species of the genus *Hypoaspis* and the non-predatory mite, *Thyreophagus entomophagus* (Lab.), in cultures of *G. psylloides.*

Eichler (1939) records that *N. hololeucus* is attacked by the gregarine, *Gregarina latifolia* Braune, and a rare unidentified species. He states that half the *N. hololeucus* in Germany were infected and that heavy infestations probably killed the host.

The disease of *N. hololeucus* and *T. globulus* recorded in this paper could not be identified as of sporozoan origin and is therefore considered to be a bacterial or virus infection.

Disease.

In cultures of *T. globulus* and *N. hololeucus* a very high mortality among the larval and pupal stages was caused by disease, the presence of which was indicated by dried up dead larvae and dead, black mushy pupae. In experimental work, eggs were separated from both the food and most of the frass of the parents by sieving, and then, after hatching, isolated larvae were bred. In these circumstances, mortality has been low—about the same as for other Ptinid species, but has been higher where larvae were bred in groups of ten. Good cultures have been obtained by separating eggs from the parental food and frass, so that the offspring had no direct contact with their parents or with older larvae. This was less successful when it was impossible to remove parental frass completely, so it is probable that the disease is acquired by eating infected frass with food.

An unsuccessful attempt has been made to infect *P. tectus* with disease from *T. globulus.* Also during culture operations, small quantities of frass from cultures of *T. globulus* and *N. hololeucus* were added to cultures of other Ptinids, including *P. tectus*, *P. fur* and *P. sexpunctatus.* No ill effects were noticed.

Statistical Methods and Value of Results.

Statistical methods.

The results presented in this paper are principally figures representing mean developmental periods and adult weights of insects bred in specified constant environmental conditions. The usual methods of obtaining the variance (V) of a sample of a population and the standard error (S.E.) of the mean (M) as given by Fisher (1946) are used throughout viz. :—

$$V=\frac{\Sigma\,(x-x)^2}{N-1}\text{ and S.E.}=\sqrt{\frac{V}{N}}$$

where N=the number of observations, x=an observation and $\overline{x}$=mean of all observations.

To test the significance of the difference between the means of two samples, *i.e.* the probability (P) that two samples came from populations with the same mean, the " t " (k) test as presented by Treloar (1939) was used together with the table of " t " from Fisher (1946), p. 174.

$$t=\frac{\bar{x}_1-\bar{x}_2}{\sqrt{S.E.^2_1+S.E.^2_2}}$$

Where differences between the means of more than two groups were tested simultaneously in an experiment, the analysis of variance as described by Mather (1949), Chapter VI, was used. Tables XI and XII (p. 42) from Fisher and Yates (1938) were used for angular transformation of results expressed as percentages.

Value of Results.

In using statistical methods with the results obtained for the length of developmental stages, it must be noted that the experimental methods used automatically group the information into units of days. The standard deviation ($\sqrt{V}$) of the grouped data of egg, pupal and other short periods is normally very small and differences between the means of such groups are normally less than a day. With such coarse grouping and short periods the " t " test is not strictly valid and may not reveal real differences present in the results. Where, even with this coarse grouping, results are statistically different this is pointed out in the following pages.

Every effort was made to ensure that all experiments made under a given set of conditions were comparable, but for some experiments, indicated in the tables, all conditions were not the same or the experiments were not concurrent. In these, some statistically significant differences occurred. For instance, in two experiments with *G. psylloides* at 20°C., both development period (fig. 1) and weight of female beetles (Table VII) differed significantly. In these experiments the insects were offspring of different groups of parents and their development periods only partly overlapped. In general, experiments at a given temperature were run concurrently to avoid the effect of small temperature and humidity variations. Such experiments gave consistent results, but if they were repeated, significantly different results might be obtained.

The Life-cycle.

The life-cycle of Ptinids can be conveniently considered in two parts, the developmental stages and the free adult life, which are dealt with separately in this paper.

The development period is fairly long in comparison with some other stored products species and the free adult life is longer, frequently very much longer, than the development period. Eggs are laid throughout most of the adult life. The insect feeds in the adult as well as in the larval stage. No significant difference between the development periods of the sexes has been noticed, but the mean length of adult life of the female exceeds that of the male (Table XII). Table XIV summarises the total length of the life-cycle of the female, the various developmental stages and the adult life of the female. The life-cycles of the five species dealt with are all very similar to that of *P. tectus.*

In storage places, adult beetles and all developmental stages may be found together throughout the year.

Development.

Methods and apparatus.

The method of rearing cultures is given by Howe (1949a). All species were bred in cultures on wheatfeed (middlings), flour or fishmeal, with or without the addition of 5 per cent. by weight of yeast. The humidity varied between 60 and 80 per cent. R.H. and the temperature was uncontrolled for all species except *G. psylloides,* which was cultured at 25°C. and 70 per cent. R.H. Groups of adult beetles bred in this manner were used to provide eggs for the experiments on development.

The experimental temperatures used were 40°±0·5°C., 35°±0·5°C. and 30°±1°C. in incubators ; 33°±0·5°C., 25°±0·5°C., 23°±0·5°C. and 19·7°±0·5°C. (hereinafter called 20°C.) in constant temperature rooms. At all temperatures except 23°C., relative humidities of 70 and 50 per cent. were maintained in desiccators using caustic potash of specific gravity 1·238 and 1·330 respectively. At 23°C., the room air was controlled at 70 per cent. R.H. Desiccators were aired regularly and the caustic potash renewed at intervals of about six weeks.

Unless otherwise stated, eggs were incubated in groups in 2×1-in. glass specimen tubes and the newly hatched larvae placed singly in 2×½-in. tubes using a soft paint brush. Experiments on development using more than one insect per tube were unsatisfactory as grouping retarded development (see also Gunn & Knight, 1945) to an extent dependent on the size of the group. As far as possible, at least 30 insects were used in every experiment on development periods.

The top of each tube was covered by cotton cambric held in place by a cork with a hole in the centre.

Food in excess of the amount required for complete development was provided from the beginning, except in experiments involving examinations for larval moults. In these, only a small amount of food was provided for the newly-hatched larva. The quantity was increased later according to the size of the larva, usually after each

TABLE I.

The percentage mortality in several experiments at 70 per cent. R.H.

Species	Temperature °C.	Percentage of eggs failing to hatch		Percentage of insects dying after hatching	
G. psylloides	40	100	(30)	—	
,, ...	35	83	(30)	80	(5)
,, ...	33	53	(30)	21	(14)
,, ...	30	39	(33)	13	(15)
,, ...	30	—		3	(30)
,, ...	25	28	(50)	24	(25)
,, ...	23	38	(578)	—	
,, ...	20	69	(75)	4	(23)
,, ...	20	—		2	(40)
E. hilleri	30	—		100	(31)
,, ...	25	25	(48)	20	(25)
,, ...	20	32	(100)	10	(67)
T. globulus	30	—		100	(30)
,, ...	25	17	(40)	20	(25)
,, ...	23	24	(1445)	—	
,, ...	20	21	(80)	16	(63)
S. squamosum	30	—		100	(30)
,, ...	25	46	(41)	16	(25)
,, ...	20	34	(70)	0	(45)
N. hololeucus	30	—		100	(35)
,, ...	25	18	(50)	87	(24)
,, ...	20	35	(86)	21	(56)

The numbers of insects used are in parentheses.

moult. Except in two experiments at 23°C. mentioned later, food for all experiments were stored for moisture conditioning in thin layers under the experimental conditions of temperature and humidity for at least one week.

Disturbance of the tubes during examination was kept to a minimum, especially while the larvae were spinning cocoons, because disturbance causes the formation of weak cocoons. The adult beetles were weighed at emergence from their cocoons using a balance accurate to ±0·1 mg.

Stages of development.

Table XIV summarises the development periods of the four stages, egg, larva, pupa and maturing adult. The proportions of total development occupied by each are uniform between temperatures, except that *N. hololeucus* emerges quickly from the cocoon at 25°C. which is above the optimum for this species.

The total development periods found by summing the mean lengths of the development stages in Tables II to VI do not exactly equal the mean total development periods given in these tables. The figures for each immature stage are based on all the insects completing that stage, but some of them died before becoming free adults and therefore could not be used in calculating total development periods. In addition a few larvae had extra instars.

The egg is white, quite tough and ovoid in shape. Eggs of all five species are similar in shape but there are small differences in size between the species (Pl. VII, *a*). As the eggs are sticky when laid, particles of food adhere to the egg shell and the eggs frequently stick to glass tubes but usually they can be removed with a soft paint brush without damage. Just before hatching the egg shell assumes a wrinkled appearance, and at the same time the young larvae become visible within, the mandibles being especially noticeable. The egg bursters on the ninth abdominal segment of *N. hololeucus* are described by van Emden (1946). The other Ptinids used in these experiments have a similar pair of egg bursters. Table I gives the

TABLE II.

Length in days of developmental stages of *G. psylloides* reared on fishmeal at 23°C. and 70 per cent. R.H.

Stage	Experiment A		Experiment B		Experiment C	
	N	M ± S.E.	N	M ± S.E.	N	M ± S.E.
Egg	27	14·6 ± 0·2		—	30	16·1 ± 0·1
Larva I	25	17·4 ± 0·7	12	15·6 ± 0·6	27	16·5 ± 0·5
,, II	22	18·5 ± 0·5	*11	16·4 ± 0·2	25	16·6 ± 0·3
,, extra	7	17·6 ± 1·3	2	14·0 ± 3·0	2	23·0 ± 6·0
,, III	17	29·2 ± 1·0		—		—
,, total	17	69·0 ± 2·4		—		—
Pupa	13	13·4 ± 0·4		—		—
Larva III+Pupa+Pre-emergence		—	10	51·1 ± 1·0	22	51·8 ± 0·5
Egg laid to adult ...	13	96·2 ± 2·6		—		—
Egg laid to adult emerged from cocoon		—	10	97·9†	22	102·2 ± 1·7

The food used for experiments B and C was not conditioned to humidity before use, but it can be assumed to have come rapidly into equilibrium with 70 per cent. R.H.

*One larva II of 46 days omitted.

†Egg period of 15·4 days (from another experiment) was added to the period " egg hatching to emergence of adult from its cocoon."

Difference for the egg between A and C is statistically significant. Differences for larva II between A and C, and between A and B are statistically significant.

mortality in the egg stage. In some experiments there was considerable mortality, which may have been due to some extent to newly-hatched larvae puncturing unhatched eggs while eating food stuck to the shells. Larvae have not been seen attacking the egg itself.

The larva is white and scarabaeiform. Sometimes the food in the gut is visible as a dark median dorsal line. The larvae of all the species except *E. hilleri* are described in a key to the larvae of the Ptinid beetles by Manton (1945). No differences, except of size, can be seen with the naked eye between larvae of different species (Pl. VII, *b*).

The appearance of larvae just before and just after each moult is characteristic (Pl. VII, *d*). Just before a moult the head capsule is much narrower than the diameter of the body and the body is sparsely hairy. Just after a moult the new head capsule is about as wide as the diameter of the body and the body appears very hairy.

For each species the lengths of larval instars were determined under at least one set of conditions (Tables II–VI). Kemper (1939) records that larvae of *N. hololeucus* normally pass through three instars. A small number of individuals had one or more extra moults, one *T. globulus* having as many as four extra instars (Table IV). Their occurrence, when frequent, is taken to indicate unfavourable conditions of food or humidity. The death rate of individuals having extra instars is high. Fishmeal, which was used for the experiments with *T. globulus* mentioned above (Table IV), was later shown to be a poor food for this species (fig. 3). Kemper (1935) records that badly fed larvae of *N. hololeucus* moulted four times instead of three. Low humidity greatly increases the number of extra moults of *P. tectus*. Azab (unpublished thesis, London Univ., 1943) found that the number of moults of *Stegobium paniceum* (L.) was generally increased by low humidity, except at 30°C., where the number decreased with humidity ; low temperature increased the number of moults, and there were more with foods on which development was slow. For all the species, the development period of the first larval instar was approximately equal to the second, but, as in *P. tectus* (Howe, 1943), the third was considerably longer.

TABLE III.

Length in days of developmental stages of *E. hilleri* at 25 °C. and 70 per cent. R.H.

Stage	Synthetic diet		Flour		Flour+5 per cent. yeast	
	N	M ± S.E.	N	M ± S.E.	N	M ± S.E.
Egg	11	8·3 ± 0·2		—		—
Larva I	36	8·0 ± 0·1	9	8·1 ± 0·2	8	7·5 ± 0·2
,, II	36	7·7 ± 0·1	8	9·0 ± 0·6	8	7·1 ± 0·1
,, III	32	17·8 ± 0·6	7	16·0 ± 0·4	8	14·5 ± 0·3
,, total	41	33·0 ± 0·6	7	33·0 ± 1·1	8	29·1 ± 0·2
Pupa	39	6·8 ± 0·1	4	6·8 ± 0·9	8	6·4 ± 0·5
Egg hatched to adult ...	39	39·8 ± 0·6	4	38·8 ± 0·7	8	35·5 ± 0·5

Differences between foods were significant as follows :—flour + yeast *cf.* both flour and synthetic diet : all except larva I and pupa ($P<\cdot01$) : synthetic food *cf.* flour : larva II ($P=\cdot05$), larva III ($P=0\cdot01$).

The total larval period of *N. hololeucus* given in Table VI is very much longer than that in another experiment shown in fig. 3 under similar physical conditions and the beetles were much lighter. This was probably caused principally by disturbance of larval feeding when looking for moults. In addition, the egg incubation period is a day longer ($P<0\cdot01$) which suggests that some other factor is also involved.

TABLE IV.

Length in days of developmental stages of *T. globulus* reared on fishmeal at 23°C.

Stage	50 per cent. R.H.		70 per cent. R.H.		P
	N	M ± S.E.	N	M ± S.E.	
Larva I	23	20·6 ± 1·0	28	16·9 ± 0·3	0·01
,, II	21	21·3 ± 1·4	26	25·8 ± 0·8	0·01
,, extra i	10	26·3 ± 2·3	12	25·7 ± 1·5	0·8
,, ,, ii	2	34·0 ± 4·0	2	37·0 ± 11·8	0·8
,, ,, iii	—		2	30·5 ± 4·5	
,, ,, iv	—		1	40·0 —	
,, III	12	39·3 ± 3·3	15	40·3 ± 3·6	0·8
,, total*	9	94·6 ± 5·1	13	91·1 ± 5·1	0·6
,, total	12	101·4 ± 6·8	15	109·9 ± 7·2	
Pupa	9	12·9 ± 0·4	8	11·6 ± 0·5	0·1–0·05
Pre-emergence	10	4·0 ± 1·0	4	2·7 ± 0·8	
Egg hatched to adult emerged from cocoon	10	116·0 ± 7·3	9	106·2 ± 5·9	0·3
Developmental mortality	46 per cent.		41 per cent.		

*Based on individuals which became adult, *i.e.*, omitting those dying as pupae.

Similar comparisons between data for other species cannot be made because different foods were used in each experiment.

Small amounts of silk are spun by the feeding larva, principally in the third instar, often in the form of a feeding cocoon.

The larva can wander, and newly hatched larvae in an empty tube normally do so, but when sufficient food is present there is usually little wandering until, in the late third instar, the larva stops feeding and wanders in search of a site in which to build its cocoon. Hickin (1941a) states that *Gibbium* does not wander. The wandering larva can bore through sacking, cardboard and paper wrappings in search of a suitable pupation site and may even enlarge cracks in wooden structures. In storage places, the cocoon is fixed to the internal surface of the sack or packet containing the food or spun in crevices, such as between floorboards or containers. Those individuals feeding on rat droppings normally pupate inside the dropping. In the laboratory, the larva usually spins against the sides of the glass tube, most frequently where the sides join the bottom. *G. psylloides* usually spins silk on the glass so that the insect inside the cocoon cannot be seen ; *S. squamosum* spins less

TABLE V.

Length in days of developmental stages of *S. squamosum* reared on fishmeal at 70 per cent. R.H.

Stage	25°C.		23°C.	
	N	M ± S.E.	N	M ± S.E.
Egg	11	14·0		—
Larva I	9	15·6 ± 0·4	26	17·6 ± 0·5
,, II	9	13·4 ± 0·6	25	17·9 ± 0·5
,, extra	4	8·3 ± 0·9		—
,, III	4	35·0 ± 5·2	10	36·4 ± 1·7
,, total	4	67·8 ± 3·7	10	74·7 ± 1·9
Pupa		—	4	15·0 ± 1·7

P (larva totals) = 0·1, difference not significant.

TABLE VI.

Length in days of developmental stages of *N. hololeucus* reared on wheatfeed at 20°C. and 70 per cent. R.H.

Stage	N	M ±S.E.
Egg	47	15·3 ±0·3
Larva I	17	22·9 ±0·6
,, II	16	24·9 ±1·6
Extra i	4	26·7 ±5·6
,, ii	2	26·0 ±2·0
Larva III	12	63·2 ±4·5
Larva total	28	109·8 ±3·6
Pupa	10	14·9 ±1·4
Pre-emergence	8	13·2 ±3·3
Egg laid to adult emerged from cocoon	32	145·0 ±2·5
Weight of female beetles in mg. ...	16	7·82 ±0·40
,, ,, male ,, ,, ,, ...	11	5·97 ±0·44
Developmental mortality after hatching		23·8%

TABLE VII.

The weights (in milligrams) of adult beetles of the five species reared on wheatfeed at 70 per cent. R.H., and over a range of temperatures.

Species	Temp. °C.	Female beetles N	Female beetles M ±S.E.	Female beetles P	Male beetles N	Male beetles M ±S.E.	Male beetles P	Comparison of ♀ and ♂ P
G. psylloides	35	—	—	—	1	2·90		—
,,	33	8	4·35 ±0·10		3	3·30 ±0·06		<·01
				·2			·1	
,,	30	7	4·14 ±0·12		6	3·57 ±0·15		<·01
				·3			·2	
,,	,,	15	4·33 ±0·12		11	3·85 ±0·13		·01
				·1			·2	
,,	25	10	4·00 ±0·15		9	3·63 ±0·12		·05
				·02			·5	
,,	20	14	4·51 ±0·16		7	3·47 ±0·23		<·01
				·05			·7	
,,	,,	33	4·10 ±0·10		29	3·39 ±0·08		<·01
E. hilleri	25	8	2·39 ±0·09		10	2·08 ±0·07		·02
				>·9			·7	
,,	20	30	2·39 ±0·06		28	2·04 ±0·05		<·01
T. globulus	25	17	3·70 ±0·14		3	3·37 ±0·04		·05
				<·01			<·01	
,,	20	28	4·37 ±0·13		21	3·69 ±0·10		<·01
S. squamosum	25	6	2·75 ±0·09		15	2·41 ±0·06		<·01
				·02			·01	
,,	20	21	2·99 ±0·06		24	2·60 ±0·05		<·01
N. hololeucus	25	1	5·1		1	5·7		—
				·01			<·01	
,,	20	26	9·06 ±0·18		17	7·92 ±0·25		<·01

All experiments at 25°C. were concurrent and conditions identical ; similarly at 20°C. and for *G. psylloides* experiments between 35° and the top 30° in the table, inclusive.

silk against the glass so that the occupant is often visible ; with *N. hololeucus, T. globulus* and *E. hilleri* the insect inside can nearly always be seen.

The cocoons vary slightly in strength, those of *G. psylloides* and *S. squamosum* being the strongest, of *E. hilleri* weaker and of *N. hololeucus* and *T. globulus* the

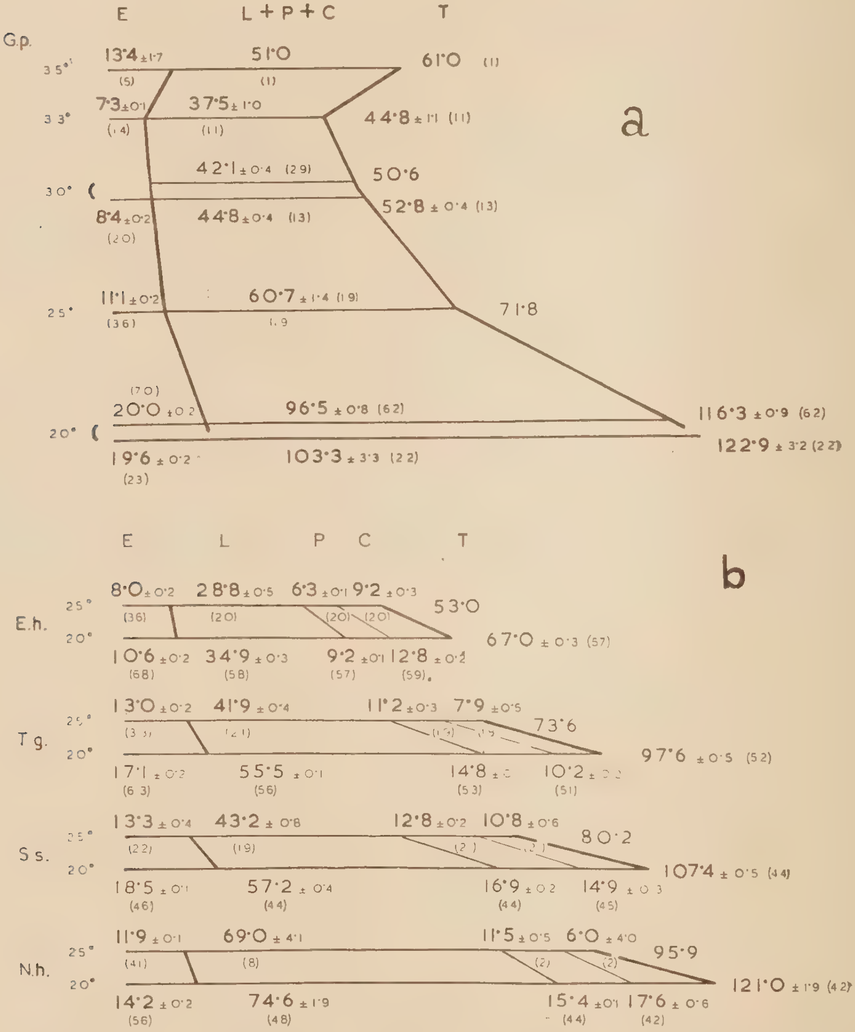

Fig. 1.—The development periods in days of the five species at 70 per cent. R.H. on wheatfeed.

G.p.=*G. psylloides*, E.h.=*E. hilleri*, T.g.=*T. globulus*, S.s.=*S. squamosum*, N.h.=*N. hololeucus*.

The mean (±standard error of the mean) for the egg (E), larva (L), pupa (P), adult in cocoon (C) and the total (T) from egg laid to emergence of the adult beetle from its cocoon are shown. The numbers of insects used are given in brackets. *G. psylloides* builds opaque cocoons so that pupation cannot be observed. The difference in total development period between the duplicate experiments with *G. psylloides* at 20° and at 30°C. are statistically significant. See also the footnote to Table VII.

weakest. Disturbance while the larva is building a cocoon sometimes causes it to abandon this cocoon and to start another. Repeated disturbance at this time may result in an extremely weak cocoon or in the larva pupating free in the food.

The pupa is soft, and white in colour at first, the shape and size varying considerably between the five species (Pl. VII, *c*). Pupal mortality is low except when pupation occurs outside the cocoon.

The maturing adult beetle remains in its cocoon for a time (pre-emergence period) while its cuticle hardens and the beetle attains sexual maturity. This period occupies up to 19 per cent. of the complete development period but can be shortened by disturbance, for instance, by shaking the tube.

The mean weights of female beetles, on emergence from the cocoons, were consistently heavier than those of the males, the differences being frequently statistically significant.

TABLE VIII.

Development in days of *E. hilleri* reared on wheatfeed at two humidities and at two temperatures.

Stage	% R.H.	20°C.			25°C.		
		N	M ±S.E.	P	N	M ±S.E.	P
Egg	50	52	10·2 ±0·3	·2	48	10·4 ±0·1	—
	70	68	10·6 ±0·2		—	— —	
Larva	50	44	48·9 ±0·8	<·01	33	44·0 ±1·0	<·01
	70	58	34·9 ±0·3		20	28·8 ±0·5	
Pupa	50	44	9·1 ±0·1	·6	30	7·0 ±0·1	<·01
	70	57	9·2 ±0·1		20	6·3 ±0·1	
Pre-emergence	50	43	12·7 ±0·3	·9	31	10·2 ±0·4	·2
	70	59	12·8 ±0·2		20	9·2 ±0·5	
Egg hatched to adult emerged from cocoon	50	44	70·5 ±0·9	<·01	30	60·3 ±0·7	<·01
	70	57	56·9 ±0·1		19	45·0 ±0·5	
Egg laid to adult emerged from cocoon	50	44	82·2 ±1·0	<·01	29	71·6 ±0·9	—
	70	57	67·0 ±0·3		—	— —	
Weight of female beetles in mg.	50	21	1·55 ±0·07	<·01	12	1·38 ±0·07	<·01
	70	30	2·39 ±0·12		8	2·39 ±0·08	
Weight of male beetles in mg.	50	24	1·31 ±0·03	<·01	21	1·12 ±0·03	<·01
	70	28	2·04 ±0·08		10	2·08 ±0·08	
Mortality	50		12%			27%	
	70		10%			20%	

All four experiments concurrent.

Effect of temperature.

The appropriate results are summarised in fig. 1 and Tables I, VII & XIV.

G. psylloides has the highest temperature range for development. The optimum temperature for rapid development of this species is close to 33°C., and 35°C. is the highest temperature at which complete development is possible.

The temperature ranges of *S. squamosum*, *T. globulus* and *E. hilleri* are similar to each other. The maxima for complete development are between 25° and 30°C. Development was significantly quicker at 25° than at 20°C. for these three species (fig. 1), hence their optima for rapid development are considered to be near 25°C. Larval development of *S. squamosum* was quicker at 25°C. than at 23°C. (Table V).

Extra, but not strictly comparable, information given below places the optima for *E. hilleri* and *T. globulus* between 23° and 25°C.

At 23°C. some experiments were performed on the development of *E. hilleri* in groups, with an ample supply of wheatfeed provided. The results were :—

		N	M ±S.E.
10 eggs per tube:	egg+larva	38	37·9 ±0·3
	pupa	38	8·9 ±0·1
	pre-emergence	37	11·6 ±0·2
	egg laid to adult emerged	37	58·4 ±0·3
6 eggs per tube:	larva	17	32·4 ±0·4

Breeding in groups is known to lengthen development (Gunn & Knight, 1945) and if the effect of grouping in this experiment is assumed to retard larval development by four to five days, then the rates of development at 23° and 25°C. are approximately equal.

On fishmeal *T. globulus* was found to develop significantly more quickly at 23° (Table IV) than at 25°C. (fig. 3, P=0·02). Since this species develops poorly on fishmeal and different consignments of this somewhat variable food had to be used these results are presented with caution.

N. hololeucus has the lowest temperature range. It developed more quickly at 25°C. than at 20°C. but the high mortality at 25°C. (Table X) shows that this temperature is near the maximum that allows complete development. The optimum is presumed to be just above 20°C.

In general, beetles bred at lower temperatures are heavier than those bred at higher temperatures. The weights of female beetles of *G. psylloides* are irregular and the weights of the male beetles (Table VII) are greatest at about 30°C.

Effect of humidity.

Very few experiments were performed with these five Ptinids at humidities other than 70 per cent. R.H.

The effect of relative humidity on the hatching of eggs of *E. hilleri* has been determined at 20°C. using relative humidities of 90, 70, 50 and 30 per cent. Four batches were shared between each humidity so that 16 groups, containing between 12 and 48 eggs were used. About 100–125 were used in all at each humidity.

At 30 per cent. R.H. an average of 30 per cent. of the eggs hatched but at higher humidities more than 70 per cent. hatched. The results at higher humidities were consistent but those at 30 per cent. R.H. were more variable (fig. 2). The percentage hatch recorded at 30 per cent. R.H. was significantly less than at other humidities (P=0·01) when the results were subjected to angular transformation, and tested by an analysis of variance.

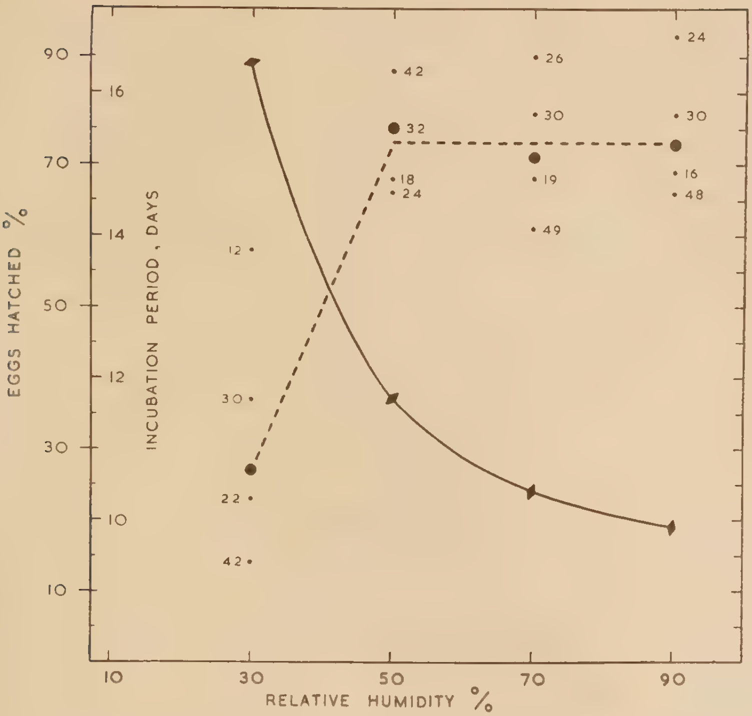

Fig. 2.—Percentage eggs hatched and incubation period of *E. hilleri* at 20°C. Small dots (.) represent the percentage eggs hatching, the number of eggs used in each experiment being given by the side of each dot. The large dots (●) show the mean percentage hatching at each humidity. The unbroken line shows the incubation period (mean of four experiments) at each humidity.

The length of the egg incubation period increased with the lowering of humidity :—

M ±S.E.
9·9 ±0·1 days at 90 per cent. R.H.
10·4 ±0·1 ,, ,, 70 ,, ,, ,,
11·7 ±0·2 ,, ,, 50 ,, ,, ,,
16·4 ±1·0 ,, ,, 30 ,, ,, ,,

The differences are all significant (using the " t " test with an analysis of variance). The validity of these tests for such results may be doubtful (see p. 156).

Development of *E. hilleri* was compared at 50 and 70 per cent. R.H. on wheatfeed at both 20° and 25°C. (Table VIII). At the lower humidity, the development period of the larva was significantly increased and the weight of the beetles significantly decreased.

Experiments carried out with *T. globulus* (Table IV) were unsatisfactory because the food used, fishmeal, was a poor one for this species and masked the effects of humidity. The first instar passed more quickly at the higher humidity, 70 per cent. R.H., but the second more quickly at the lower humidity, 50 per cent. Some larvae had several extra moults at 70 per cent. R.H. and, after a prolonged larval life, died as pupae. If a comparison is made of the larval development period of only those individuals which became adult, the period at 70 per cent. R.H. is slightly the shorter. The pupal period was also slightly shorter at the higher humidity.

Hickin (1941a) found that *G. psylloides* could not complete development at 27°C. and 30 per cent. R.H. He found that the rate of development was much the same at 40, 50 and 60 per cent. R.H., but his quickest rate was considerably slower than any reported here. Since he failed to obtain eggs at higher humidities, it seems that there must have been some defect in his environmental conditions sufficient to invalidate his results.

The effect of humidity on these three species is similar to that obtained with more extensive experiments for *P. tectus*. The lower humidity limit of 40 per cent.

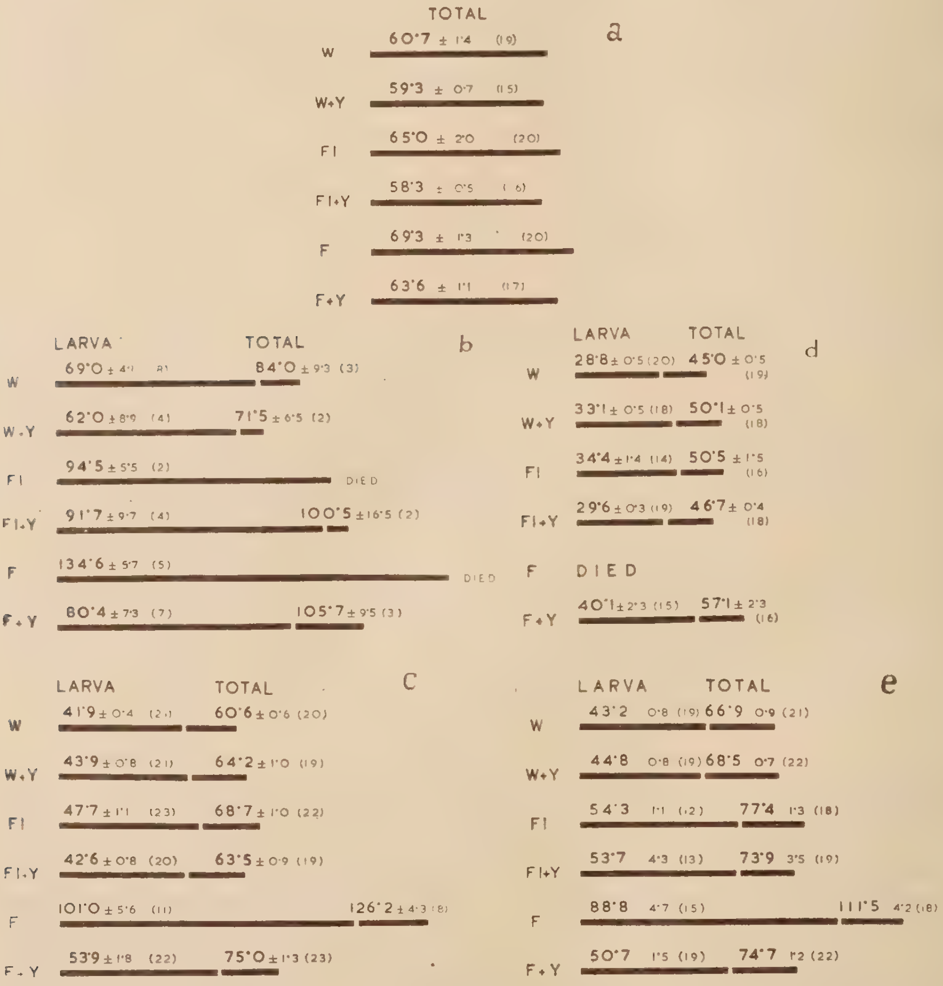

Fig. 3.—The development period in days at 25°C. & 70 per cent. R.H. and the total from egg hatching to emergence of adult from its cocoon for (a) *Gibbium psylloides* ; (b) *Niptus hololeucus* ; (c) *Trigonogenius globulus* ; (d) *Eurostus hilleri* ; (e) *Stethomezium squamosum* on wheatfeed (W), flour (Fl) and fishmeal (F) with and without yeast (Y) added.

R.H. for that species may be near the limits for the five species discussed in this paper.

Food.

1. *The range of foodstuffs.*—A survey of the records in the literature of substances on which a pest has been found is generally misleading, as insects often spread to substances on which they cannot subsist. It is clear, however, that the three Ptinids, *G. psylloides*, *N. hololeucus* and *T. globulus* can live on a wide range of foodstuffs of both plant and animal origin and that they are often scavengers but seldom major primary pests.

Laboratory tests with *G. psylloides*, *S. squamosum* and *T. globulus* have confirmed that these species are able to develop on a wide range of foodstuffs. Table IX gives a list of foods tried, their composition and the success of each Ptinid in developing on them. The main factors inhibiting growth were the physical unsuitability of the food and the absence of certain accessory food factors. Thus there was no development on either dried beef or dried herring meal which were very greasy foodstuffs. Even mixing fishmeal in equal quantities with herring meal did not allow of development. Similarly development was not possible on foods containing much hygroscopic sugar. Ground onion, for instance, became very sticky and wet.

In general, development was quicker on fine foodstuffs than on foods composed of course or hard particles (see also Howe, 1949b), but *G. psylloides* often developed more quickly on strips of dried vegetable inside which some larvae were protected from disturbance.

The effect of accessory food factors was demonstrated when the addition of yeast permitted development where otherwise none was possible. The addition of yeast also accelerated development on almost all foodstuffs (fig. 3).

E. hilleri and *N. hololeucus* were not tested on the dehydrated foods. *E. hilleri* will not breed on fishmeal unless yeast is added but does well on flour, wheatfeed and dehydrated potato. *N. hololeucus* succeeded on fishmeal but not as well as on grain products.

2. *Comparison of fishmeal, flour and wheatfeed.*—The standard foods used for laboratory culture of the various Ptinids have been fishmeal, wholemeal flour, and wheatfeed. It was evident that while wheatfeed was adequate for all species fishmeal was unsuitable for some.

A detailed experiment was carried out at 25°C. and 70 per cent. R.H. to test these three foods on the five species concerned. In addition, a parallel experiment was performed in which 5 per cent. by weight of dried brewer's yeast was added to make up any possible deficiency in B vitamins. Twenty-five individuals of each species were used for each food, and were allocated between four desiccators. The desiccators were kept close together in a constant temperature room at 25°C.

Results of these experiments are summarised in Table X and fig. 3.

N. hololeucus does not develop satisfactorily at 25°C. but the limited results indicate that of the three foods without added yeast wheatfeed is the best for this species, no individuals completing development on the other foods. The remaining four species all developed most quickly on wheatfeed. *E. hilleri* was unable to develop on fishmeal and for all other species the difference between development periods on wheatfeed and fishmeal were statistically significant. Except with *G. psylloides* development was significantly quicker on wheatfeed than on flour and significantly quicker on flour than on fishmeal.

The differences of adult weight at emergence from the cocoon were not marked. In general, heavy beetles were obtained under given conditions of temperature and humidity when development was fast. This is contrary to the discoveries of Gunn

TABLE IX.

Development of three species at 23°C., 70 per cent. R.H. on dried foods of which the composition is shown.

Food used for experiment	Food used for analysis	Composition (%) after conditioning to 70% R.H.							G. *psylloides*	T. *globulus*	S. *squamosum*
				Available carbohydrate							
		Water	Un-available carbo-hydrate	Sugar as invert sugar	Starch as glucose	Total as mono-sac-charides	Protein	Fat			
Fishmeal	fishmeal ...	10·0				0·0	63·5	5·9	× × × + +	× + +	× × × + + +
Dried beef ...	steak, raw ...	7·7				0·0	56·5	30·8	—	—	—
Soya bean flour ...	soya bean flour...	11·0		Trace	16·7	16·7	48·0	7·0		× × + + +	
,, ,, ,, ...	,, ,, ,, ...							1·4		× × + +	
Yeast powder ...	yeast powder ...	20·5				28·2*	42·5	1·9	× × × + +	× × + +	× × + + +
Dried egg powder...	dried egg powder	14·5				0·0	40·8	40·7	× + + +	—	—
Dried egg powder plus 5% yeast										× × + + +	
Dried herring ...	raw fillets, fresh	12·9				0·0	40·5	43·9	—	—	—
Dried milk ...	household ...	11·7				35·2	23·9	26·9	× + +	× + +	—
Dried cabbage ...	winter, raw, fresh	26·5	21·0	69·8	0·0	69·8	22·7	Trace	× × × + + +	—	× × + +
Wheatfeed ...	coarse middlings	12·7				57·7	16·8	5·2	× × × + + +	× × × + + +	× × × + + +
Toppings ...									× × × + + +	× × + + +	× + +
Wholemeal flour ...	Manitoba wheat	14·9		Trace	70·7	70·7	13·9	2·6	× × × + + +	× × + + +	× × + + +
Wheat ...	Manitoba ...								× × × + + +	× × + + +	—
Dried swede ...	raw, fresh ...	26·3	24·9	38·7	0·9	39·6	10·1	Trace	× × + +	× + +	× × + +
Dried onion ...	raw, fresh ...	30·3	13·9	55·4	0·0	55·4	9·6	Trace	× × + +	—	—
Dried beetroot ...	fresh, boiled (contains inulin)	24·2	11·6	46·1	0·0	46·1	8·4	Trace	× +	× + +	× + +
Dried potato ...	old, raw, fresh ...	12·2	7·7	1·8	74·8	76·6	7·7	Trace	× × + +	—	× + +
Dried carrot ...	old, raw, fresh ...	23·7	23·0	42·8	0·0	42·8	5·5	Trace	× × × + +	× × + +	× × + +

— No insect completed development. × 10 per cent. or fewer insects completed development. × × 11 to 50 per cent. insects completed development. × × × More than 50 per cent. insects completed development. + Development completed in more than 150 days. + + Development completed in 100 to 150 days. + + + Development completed in less than 100 days. * Indicates some fibre included. The composition of foods is taken from McCance & Widdowson (1946), Fraenkel & Blewett (1943a), Bolton (1928) and Kent-Jones (1939). The percentage composition was adjusted for water content, which was found after conditioning the food at 70 per cent. R.H., 25°C. for at least one week, using 115°C. for 4·5 hours in a ventilated oven.

and Knight (1945) for *P. tectus*. Thus ordinary wholemeal flour produced lighter adults than wheatfeed for all species, but conversely fishmeal produced heavy adults of *G. psylloides*. Only one difference was significant, that between wheatfeed and fishmeal for *T. globulus*.

These differences in development and weight may be due to food deficiencies or to the nature of the food, animal (protein) or plant (carbohydrate and plant protein). The importance of these factors is shown by the results of experiments with the inclusion of yeast.

The addition of yeast to fishmeal and to flour accelerated development of all species. A few *N. hololeucus* survived on both foods plus yeast and development of *E. hilleri* on fishmeal plus yeast was possible. By the addition of yeast to fishmeal, the development period was significantly decreased for the other three species and mortality much reduced for *S. squamosum* and *T. globulus*. The development period on flour was significantly shortened for *E. hilleri*, *G. psylloides* and *T. globulus* by the addition of yeast. Wheatfeed was not improved by the addition of yeast, which increased the development period of *S. squamosum* and *T. globulus* and significantly increased that of *E. hilleri*.

The addition of yeast to foods produced a general increase in adult weight, some increments being significant for fishmeal and flour.

These results show that yeast makes up some deficiencies of diet in fishmeal and wholemeal flour. These deficiencies, which are not exhibited by wheatfeed, are probably in vitamins of the B group. There is evidently a marked deficiency in fishmeal, completely limiting for *E. hilleri* and serious for the other species except *G. psylloides*. Even this species is affected in developmental speed though not in weight or mortality. The deficiency in flour is less serious and the addition of yeast makes flour as good as wheatfeed, but fishmeal with yeast added remains markedly inferior.

For *S. squamosum* the development period is significantly longer on fishmeal plus yeast than on wheatfeed plus yeast ; for *E. hilleri*, *G. psylloides* and *T. globulus* it is significantly longer on fishmeal plus yeast than on either of the other foods plus yeast. *E. hilleri* developed significantly more quickly on flour plus yeast than on wheatfeed plus yeast, but no other difference between these two foods was significant. Few significant differences exist between the weights.

Since the amount of yeast added is large enough to make up the B vitamin deficiencies of the foods it is possible that the Ptinids used, except *S. squamosum*, develop better on plant than on animal materials.

3. *Synthetic diets.*—An attempt to analyse the need of some of these Ptinids for protein, carbohydrate and a sterol was made with simple synthetic diets. Using as a standard the diet introduced by Fraenkel and Blewett (1943b), the proportions of casein and glucose were varied. Five parts dried brewer's yeast and two parts McCollum's salt mixture were added to each diet and one part cholesterol to all except one " cholesterol free " diet. The proportions of glucose and casein (B.D.H. reagents) were as follows :—

Diet	Parts of glucose	Parts of casein
No glucose	0	100
High casein	25	75
Standard and cholesterol free	50	50
Low casein	75	25
Very low casein	90	10

TABLE X.

The weights (in milligrams) of adult beetles of the five species reared at 25°C. and 70 per cent. R.H. on three foods with and without yeast.

Food	Weight of female beetles				Weight of male beetles				Mortality
	N	M	±S.E.	P	N	M	±S.E.	P	Per cent.
G. psylloides									
Wheatfeed	10	4·00	±0·15	·3	9	3·63	±0·12	·4	24
Wheatfeed+yeast	5	4·18	±0·10		9	3·77	±0·12		33
Flour	9	3·87	±0·13	·02	11	3·25	±0·09	<·01	16
Flour+yeast	9	4·30	±0·11		7	3·69	±0·08		36
Fishmeal	12	4·23	±0·12	·6	8	3·50	±0·14	·4	20
Fishmeal+yeast	9	4·33	±0·16		6	3·72	±0·20		32
E. hilleri									
Wheatfeed	8	2·39	±0·08	·05	10	2·08	±0·08	·3	20
Wheatfeed+yeast	7	2·11	±0·09		10	1·92	±0·10		28
Flour	7	1·96	±0·12	<·01	7	1·80	±0·09	·1	36
Flour+yeast	5	2·52	±0·09		9	2·14	±0·15		25
Fishmeal	—	—	—	—	—	—	—	—	100
Fishmeal+yeast	9	2·04	±0·11		7	1·89	±0·14		36
T. globulus									
Wheatfeed	17	3·70	±0·14	·2	3	3·37	±0·04	·2	20
Wheatfeed+yeast	10	4·03	±0·18		9	3·51	±0·09		24
Flour	7	3·31	±0·21	·9	15	2·92	±0·07	·05	4
Flour+yeast	10	3·29	±0·13		7	3·13	±0·07		24
Fishmeal	5	2·62	±0·21	<·01	5	2·20	±0·36	·1	60
Fishmeal+yeast	15	3·44	±0·12		7	2·90	±0·12		8
S. squamosum									
Wheatfeed	6	2·75	±0·09	·6	15	2·41	±0·06	·2	16
Wheatfeed+yeast	7	2·81	±0·09		13	2·51	±0·05		12
Flour	10	2·55	±0·13	·02	8	2·44	±0·04	·4	25
Flour+yeast	7	2·96	±0·08		12	2·53	±0·11		24
Fishmeal	7	2·40	±0·13	<·01	10	2·51	±0·08	·3	28
Fishmeal+yeast	12	2·98	±0·06		9	2·68	±0·13		4
N. hololeucus									
Wheatfeed	1	5·1	—		1	5·7	—		87
Wheatfeed+yeast ...	2	6·60	±2·20		7	—	—		91
Flour	—	—	—		—	—	—		100
Flour+yeast	1	5·6	—		1	4·0	—		92
Fishmeal	—	—	—		—	—	—		100
Fishmeal+yeast	1	5·8	—		2	3·00	±0·10		88

All experiments took place concurrently.

Groups of ten newly hatched larvae were placed on 2·5 gm. of food in 2×1 in. tubes. Each diet was tested, at least in duplicate, with *G. psylloides*, *S. squamosum* and *T. globulus* at 23°C. and 70 per cent. R.H. To minimise disturbance, tubes were examined only for pupae and adults.

The results are summarised in Table XI.

TABLE XI.

Development period (egg hatched to beetle emerged from cocoon) in days at 23°C. and 70 per cent. R.H. on synthetic foods.

Food (parts casein)	*G. psylloides* 2 replicates combined N	*G. psylloides* 2 replicates combined M ±S.E.	*S. squamosum* 2 replicates combined N	*S. squamosum* 2 replicates combined M ±S.E.	*T. globulus* 4 replicates combined N	*T. globulus* 4 replicates combined M ±S.E.
50 without sterol	7	100·0 ±3·8	9	89·9 ±2·0	8	108·1 ±4·7
100 with ,,	16	93·1 ±1·4	16	81·9 ±0·7	17	101·9 ±3·0
75 ,, ,,	16	93·1 ±1·1	6	96·3 ±4·5	14	101·8 ±1·1
50 ,, ,,	14	87·9 ±1·3	18	82·9 ±0·9	24	97·9 ±1·8
25 ,, ,,	17	85·1 ±0·9	6	93·2 ±3·5	15	92·5 ±1·6
10 ,, ,,	16	90·7 ±1·2	6	94·4 ±1·7	19	106·1 ±1·7

Differences between the foods were significant in the following instances :—

Foods (parts casein)	P	Foods (parts casein)	P	Foods (parts casein)	P
25 *cf.* 10	<·01	100 *cf.* no sterol	<·01	25 *cf.* 50	<·01
,, ,, 100	<·01	,, ,, 25	<·01	,, ,, 75	<·01
,, ,, 75	<·01	,, ,, 10	<·01	,, ,, 100	<·01
,, ,, no sterol	<·01	,, ,, 75	<·01	,, ,, 10	<·01
				,, ,, no sterol	<·01
50 *cf.* 100	<·01	50 *cf.* no sterol	<·01		
,, ,, 75	<·01	,, ,, 25	<·01	50 *cf.* 10	<·01
,, ,, no sterol	<·01	,, ,, 10	<·01	,, ,, no sterol	·05
		,, ,, 75	<·01		
10 *cf.* no sterol	·02			75 *cf.* 10	·05

A wide range of protein-carbohydrate ratio was tolerated. Although the replicates were concurrent and comparable, there was a significant difference between the replicates of *G. psylloides* on the diet containing 10 parts casein. Development was quickest on diets containing 25 and 50 parts of casein. The replicates for *T. globulus* were much more variable, significant differences being frequent and mortality very high, some tubes becoming infested by mites (*Glycyphagus destructor*). However, the results were similar to those for *Gibbium psylloides*. The experiments with *S. squamosum* also became infested by mites and there was a significant difference between the replicates on the food with no sterol : the results were inconsistent as the insects did well on diets containing 100 and 50 parts casein, but not on the diet with 75 parts casein.

For all three species development was considerably delayed and mortality was high when no sterol was supplied in addition to yeast.

In general, the best results with these diets were superior to fishmeal, but not so good as wheatfeed.

E. hilleri did well on the standard synthetic diet (Table III).

TABLE XII.

Egg output and adult life at 25°C. and 70 per cent. R.H. on wheatfeed.

Species	Adult life in weeks				Sign. of diff. between sexes	Total egg-output per female		Range of egg output of individual females
	Female		Male					
	N	M ± S.E.	N	M ± S.E.	P	N	M ± S.E.	
E. hilleri	7	18·7 ± 0·8	7	16·0 ± 1·6	·1	7	15·3 ± 4·8	1 to 33
N. hololeucus	30	16·3 ± 1·2	31	11·4 ± 1·4	·01	15 20	16·0 ± 3·2 P·01 46·2 ± 8·7	2 to 48 5 to 151
T. globulus	24	36·7 ± 1·4	16	33·7 ± 2·1	·3	24	161·7 ± 25·5	22 to 417
S. squamosum	24	30·8 ± 2·3	19	25·6 ± 2·7	·1	24	168·8 ± 23·5	17 to 376
G. psylloides	5 28	49·2 ± 1·3 P·01 41·6 ± 1·7	4 26	10·6 ± 0·1 P·01 25·5 ± 3·1	·01 ·01	34	283·1 ± 24·8	45 to 524

The Free Adult Beetle and Egg Production.

Distinctions between sexes.

Where external differences between the sexes occur, they are given by Hinton (1941) *viz.* :—*E. hilleri*, the female has a brush of long, erect hairs arising from a large shallow oval puncture on each side of the middle apical region of the fifth abdominal sternite : *G. psylloides*, the female lacks a large round puncture and an erect brush of compact hairs on the middle of the metasternal disc : *T. globulus*, the female lacks a median, setiferous puncture on the posterior fifth of the metasternal disc and the metasternum is shorter in the female than in the male.

Pupae may be sexed in the usual way for beetles, but some pupae of *T. globulus* prove difficult.

Methods used for oviposition experiments.

The adult beetles require food and lay their eggs over several months. The adult life and egg output has been investigated using individual female beetles. They were kept, each with a male, in 2×1 inch specimen tubes containing food passed through a sieve of 60 meshes to the inch. Eggs were retained in the sieve when the food was sieved once or twice weekly. As adults can sometimes climb clean glass, each tube was closed with cotton cambric held in place by a cork through which a hole had been bored. The beetles need free water to drink for the maximum number of eggs to be laid. This was provided by placing them on moist cotton wool for about three hours after each sieving. In the experiments with the two species having no obvious external sex differences, beetles were paired at random and only those pairs producing eggs were retained. Sterile pairs of the other three species were also discarded.

Length of adult life.

Table XII summarises the length of adult life and egg output at 25°C. and 70 per cent. R.H.

Two separate groups of adults from different cultures were used for *N. hololeucus*, *S. squamosum* and *G. psylloides*, but the results for the two groups have been combined except where the differences between the groups are statistically significant.

There are considerable differences in the length of adult life between the five species, due, to some extent, to the temperature used being optimal for one species and a little high for the others. As 25°C. is the maximum temperature for complete development of *N. hololeucus*, this temperature is probably too high for a long adult life of this species. Two pairs of beetles of this species were kept at 20°C., the females living 23 and 24 weeks and the males 2 and 22 weeks. The optima for long adult life of *S. squamosum* and *T. globulus* are probably below 25°C., but that for *G. psylloides* is probably near 25°C. The length of adult life for *G. psylloides* given by Hickin (1941a), namely 30 to 40 weeks at 27°C., agrees with the results for the larger group of beetles in Table XII.

In general female beetles lived longer than males (*cf.* Hickin, 1941a) the difference being statistically significant for *G. psylloides* and *N. hololeucus*.

Egg production.

Before oviposition begins there is a short period (the pre-oviposition period) during which copulation takes place and the eggs are fertilised. After this period oviposition begins and the rate of egg output increases rapidly to reach a maximum within a few days except in the case of *E. hilleri*, then slowly decreases as the beetles age (fig. 4). Frequent copulation is probably necessary throughout the long oviposition period for maximum egg production to be attained. In experiments, food was renewed at intervals and, in three out of the eight instances recorded, the

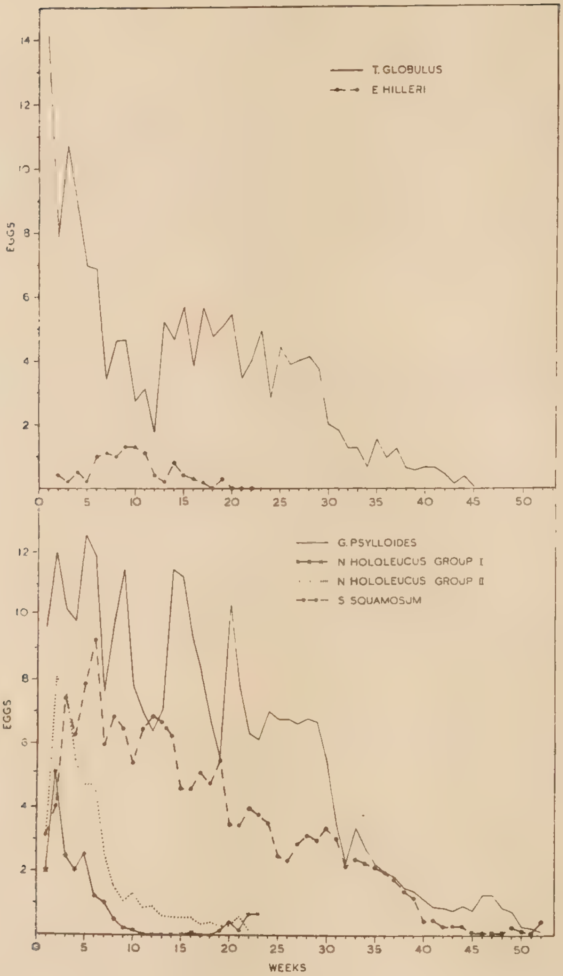

Fig. 4.—Weekly rate of egg production at 25°C. and 70 per cent. R.H. on wheatfeed. For *N. hololeucus* there was a significant difference in the mean total egg production between the two groups of adults, I and II, which are shown separately. There were no significant differences between the groups for the other four species so the two groups for each of these are combined. The number of adults for each species on which the results are based are given in Table XII, the number of eggs being the mean rate of egg output per original female for each week.

rate of oviposition markedly increased after the addition of new food. Hence, ideally, the food should be renewed at every sieving.

The total egg-output at 25°C. differed greatly between the species (Table XII). These differences may be due to the experimental temperature being about optimal for the total egg-output of *G. psylloides*, above the optimum for *S. squamosum*, *T. globulus* and *E. hilleri* and considerably above that for *N. hololeucus*. Two pairs of *N. hololeucus*, kept at 20°C., laid 223 and 81 eggs, both numbers being much greater than the average at 25°C. The weekly rate of oviposition was also much greater than that for 25°C. shown in fig. 4. Marcus (1929) reported an average egg output of 25 to 30 eggs in 3 to 5 weeks in unspecified conditions. This small number is probably due to lack of free drinking water. Experience has shown that lack of water considerably reduces egg-output.

In addition to the group of *E. hilleri*, shown in Table XII, which laid very few eggs in comparison with the other species, two additional groups of 30 and 26 pairs of beetles from different insectary cultures were used. These, however, laid no eggs although the experimental conditions were similar.

E. hilleri was first found in this country in 1939 and spread rapidly to widely separated areas (Hinton, 1941). This suggests that either the field insects were more fertile than beetles used in the laboratory, or that the laboratory conditions and technique used were not suitable for good egg production. These experimental results for *E. hilleri*, therefore, must be accepted with caution.

At 27°C. and 70, 80 and 90 per cent. R.H., Hickin (1941a) found that *G. psylloides* laid no eggs, probably again because no drinking water was supplied.

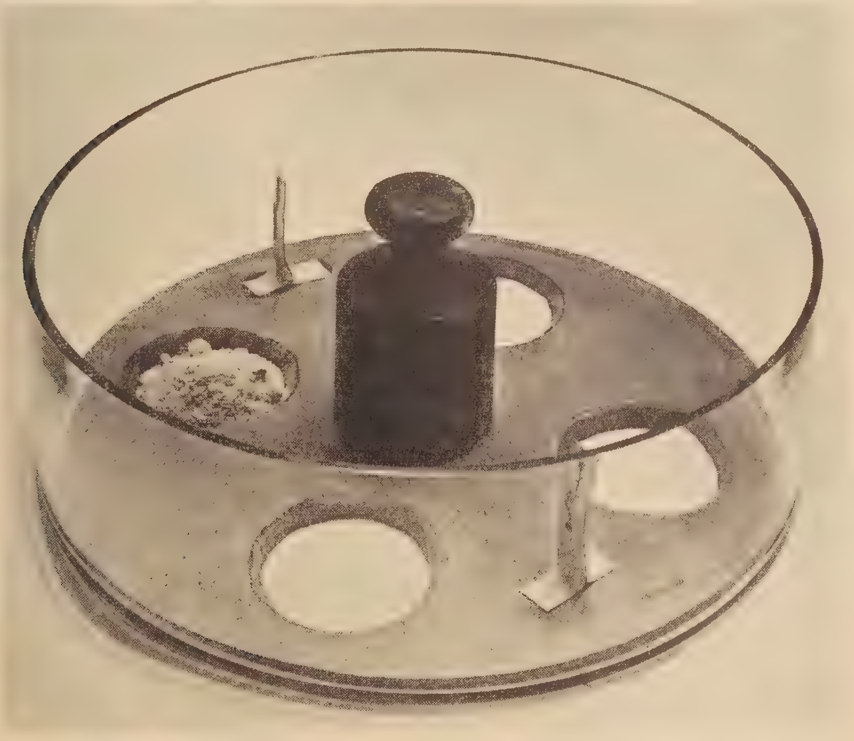

Fig. 5.—The apparatus used for the experiments on the choice of foods for oviposition. Food has been placed on one filter paper on the left. See text for details.

Oviposition site.

Beetles of all five species are active in dim light and normally lay their eggs in food. Beetles have frequently been placed in an empty glass jar with or without dry or moist blotting paper and in these conditions no eggs were laid, but when food was added, oviposition commenced and proceeded normally. Some of these species have been recorded on textiles and they might be expected to oviposit on such materials as wool. In the laboratory, a few eggs were laid in cotton wool or in clean thick knitting wool when no food was present but the number of eggs laid was very much smaller than would have been expected in the presence of food. König (1936) and Ewer and Ewer (1942) state that, in the presence of food, *P. tectus* can readily lay eggs in wool, but, in our own experiments on *P. tectus*, oviposition in wool was very poor.

Choice of food for oviposition.

Experiments have been carried out to discover if the beetles show any preference when given a choice of foods in which to oviposit. The foods used were fishmeal, ground copra cake, wheatfeed and wholemeal flour. After conditioning at 70 per cent. R.H. and 20°C., the foods were sieved through a sieve of 60 meshes to the inch and eggs were later removed with the same sieve. The experiments were carried out in the dark at 23°C. and 70 per cent. R.H., using insects cultured at a temperature fluctuating between 15° and 18°C., and given a drink on damp blotting paper before the experiment was commenced. The apparatus used (fig. 5) consisted of a potato dish some 5 cm. deep and 25 cm. diameter. The bottom of the dish was covered by a thick piece of cardboard which fitted tightly, but could be removed by means of two handles. Four holes, symmetrically placed 5 cm. in diameter and with bevelled edges, were made in the cardboard 2 to 3 cm. from the edge. This cardboard disc was placed in the potato dish so that the holes fitted over four filter papers, each 10 cm. in diameter. Equal volumes of the test foods (a $2 \times \frac{1}{2}$ inch glass tube was used as a measure) were placed in heaps, one to each filter paper. The original positions of the foods were chosen at random, but in subsequent tests using the same piece of cardboard, the original positions were retained as the board took up the smell of the food. Only three different positions are possible if mirror image positions are excluded. The cardboard was kept in position with a

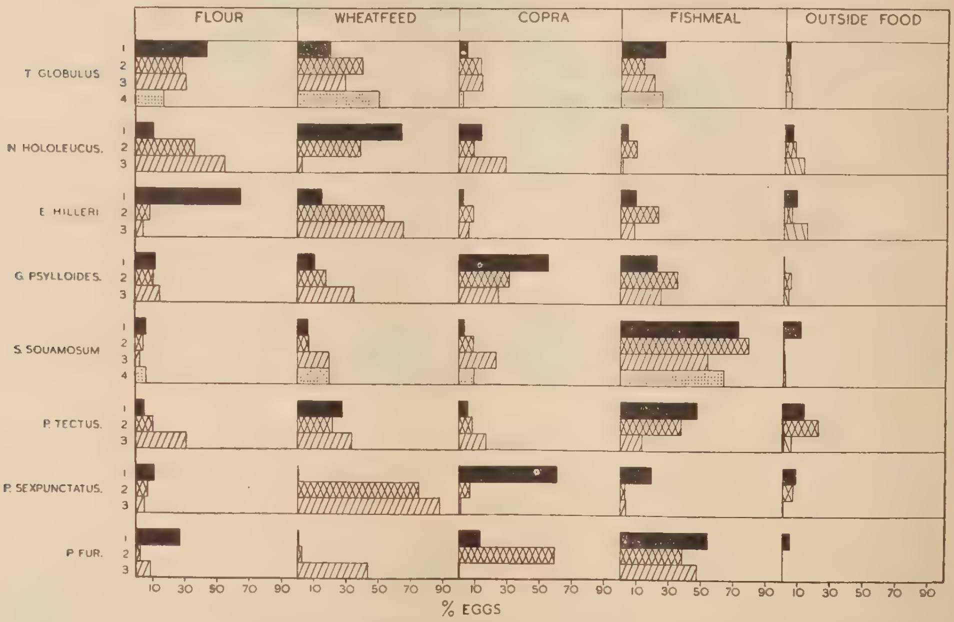

Fig. 6.—Choice of foods for oviposition, showing, in three or four experiments for each species, the distribution of the eggs between the four foods as percentages of the total eggs laid in each experiment.

½ kg. weight. One hundred adult insects were spread evenly around this, and the apparatus immediately covered by cotton cambric and black cloth, kept in place by elastic bands. The beetles were left undisturbed for a week. A small amount of food, spread on to the bevelled edges of the holes by the movement of the adults, was brushed back on to the filter papers before the board was removed. The filter papers were then taken out and the contents sieved. In the absence of the board more food is spread by the beetles' activity and more eggs are likely to be laid away from the filter papers. Even with the board present, a small proportion of eggs was laid away from the foods and could not be allocated to any particular food.

The results are shown in fig. 6 together with those for similar experiments on *Ptinus tectus*, *P. sexpunctatus* and *P. fur*. In all the experiments there is obvious divergence from the even sharing of eggs between the foods and there are some considerable differences between some of the replicates for particular species. In particular *E. hilleri* laid well once on flour, but avoided it in the two replicates ; also *P. sexpunctatus* did not lay a single egg in wheatfeed in one experiment, but laid nearly all its eggs in this food in the other two. After applying an angular transformation to the percentages of eggs laid in the foods (omitting those eggs laid outside food), an analysis of variance showed the error (variance within foods) to be small for *S. squamosum*, *T. globulus* and *G. psylloides*. This indicates that these results are reasonably homogeneous. The error was large for the other five species in fig. 6 indicating heterogeneity of results. The percentage of eggs laid by *S. squamosum* was significantly greater in fishmeal than in the other three foods ; the percentage laid by *T. globulus* was significantly smaller in copra than in the other three foods ; no other differences between foods were significant for any species, the differences for *G. psylloides* not being large enough to be significant, although the error was small.

There seems to be no relation between the choice of foods for oviposition and their suitability for development.

Effect of type of food on egg production.

The short term effect of the type of food on the rate of egg output of one species, *E. hilleri*, has been studied.

The foods used were fishmeal, ground copra cake, wheatfeed and wholemeal flour at 20°C. and 70 per cent. R.H. Four groups of 100 beetles were selected at random from cultures on wheatfeed plus yeast. The beetles were of mixed age. The experimental samples of food were ground and passed through a sieve of 60 meshes to the inch, so that eggs could easily be sieved off later. Before being placed on an experimental food, however, each group of beetles was conditioned to that food by being placed for 5½ days on an unground sample under the experimental

TABLE XIII.

The short term effect of four foods on the rate of oviposition of *E. hilleri* at 20°C. and 70 per cent. R.H.

Food	Eggs laid by the 4 groups of adults	Total	Source of variation	F	P
Copra	14, 8, 26, 13	61	between foods	6·36	·05–·01
Fishmeal	31, 64, 42, 62	199	between groups	1·97	>·05
Flour	14, 23, 76, 30	143	between days	3·20	>·05
Wheatfeed	6, 11, 34, 16	67			

P=probability that the variance attributed to foods, groups or days is due to random sampling.

conditions. Each group was then placed on moist blotting paper for ½ day and then put on an experimental sample of food for 1 day. Thus, over 4 weeks, each group of insects spent 1 week on each food, and the numbers of eggs laid on the last day of each week were counted. Each group of adults was passed from one food to another in a different order, so that for example, one group started on wheatfeed, and each of the remaining three groups was transferred to wheatfeed from one of the other three foods. The groups were kept on food in 1-lb. jam jars in a desiccator during the experiment.

The results were analysed using the analysis of variance technique and are given in Table XIII. They show a significant difference between the foods, but not between the groups of adults or the days. Three times as many eggs were laid on fishmeal as on either copra or on wheatfeed. This is surprising as *E. hilleri* cannot complete its development on fishmeal. The long term effect of food on oviposition may be very different from this short term effect, for, if fishmeal is also unsuitable for the adult beetle, the maturation of eggs may quickly cease.

The beetles used were bred on wheatfeed plus yeast, the most suitable food for this species, and laid poorly on wheatfeed in the experiment. Thus, as Crombie (1941) concluded for *Rhizopertha dominica* (F.), *E. hilleri* is not especially attracted to lay in the same type of food as that in which it was bred.

Discussion.

None of the work on the biology of the five minor Ptinid pests described above shows any marked difference from the major pest *P. tectus*. This species multiplies more quickly in warehouses than any of those studied here, because it develops more quickly than all except *E. hilleri* and lays more than twice as many eggs as the other species (see D.S.I.R., 1949, p. 8). In unheated warehouses, *P. tectus* passes two to three generations a year (Howe, 1950), whereas none of the others, except possibly *E. hilleri*, is likely to pass more than one with a few individuals completing two. Thus, these species are seldom found in large enough numbers to be considered pests, and when found are generally present as scavengers often associated with rodent droppings.

The findings of this paper show that not one of the species is likely to become more than a minor pest. *T. globulus* was first introduced into Britain about 1900 (Tomlin, 1900) (compare *P. tectus*, 1892) and is now established, but only of minor importance. *S. squamosum* has not yet been found in warehouses in Britain and is unlikely to become a pest. More doubt attaches to the assessment of *E. hilleri*. It was first found in Britain in 1939 and appeared to spread quickly for about 2 years, then control measures reduced its importance. *E. hilleri* develops more quickly than *P. tectus*, but is more limited in food range. In the laboratory it lays few eggs. If this is a fair estimate of the egg-laying ability of the species then *E. hilleri* will not become a pest, but it is possible that in the laboratory some unfavourable condition is introduced which restricts egg output. All the foregoing species have an optimum close to 23°C. *G. psylloides* requires rather higher temperatures for quick development (Table XIV) and is unlikely to become numerous in Britain. *N. hololeucus*, with a lower optimum, just above 20°C., does occasionally occur in large numbers.

A little information on the field biology of *Gibbium* spp. and a considerable amount on *N. hololeucus* is available in the literature.

Fletcher and Ghosh (1920) state that *G. psylloides* (under the synonym *G. scotias*) completes a generation in a month in the Punjab. This is less than the shortest period recorded in this paper (fig. 3) from which it seems likely that, in optimum conditions, a complete generation from egg laid to the first egg of the next generation would take about 2 months.

TABLE XIV.

A summary of the life-cycles of the five species at 70 per cent. R.H. Periods are given to the nearest day.

Temp. °C.	Species	Food	Adult life of ♀	Development period				
				Total*	Egg	Larva	Pupa	Pre-em.
35	*G. psylloides*	Wheatfeed	—	61	13 (21)	—	—	—
33	,,	,,	—	45	7 (16)	—	—	—
30	,,	,,	—	51	8 (16)	—	—	—
25	*G. psylloides*	Wheatfeed	291	72	11 (15)	—	—	—
,,	*E. hilleri*	,,	131	53	8 (15)	29 (55)	6 (12)	9 (18)
,,	*T. globulus*	,,	257	74	13 (18)	42 (57)	11 (15)	8 (11)
,,	*S. squamosum*	,,	216	80	13 (17)	43 (54)	13 (16)	11 (13)
,,	*N. hololeucus*	,,	114	96	12 (12)	69 (70)	11 (12)	6 (6)
25	*G. psylloides*	Flour	—	76	—	—	—	—
,,	*E. hilleri*	,,	—	58	—	34	—	—
,,	*T. globulus*	,,	—	82	—	48	—	—
,,	*S. squamosum*	,,	—	91	—	54	—	—
,,	*N. hololeucus*	,,	—	died	—	94	—	died
25	*G. psylloides*	Fishmeal	—	80	—	—	—	—
,,	*E. hilleri*	,,	—	died		died		
,,	*T. globulus*	,,	—	139	—	101	—	—
,,	*S. squamosum*	,,	—	125	—	89	—	—
,,	*N. hololeucus*	,,	—	died	—	135	—	died
25	*G. psylloides*	Synthetic	—	99	—	—	—	—
,,	*E. hilleri*	,,	—	57	—	33	—	—
,,	*T. globulus*	,,	—	111	—	—	—	—
,,	*S. squamosum*	,,	—	96	—	—	—	—
23	*T. globulus*	Fishmeal	—	119	—	91	12	3
20	*G. psylloides*	Wheatfeed	—	116	20 (17)	—	—	—
,,	*E. hilleri*	,,	—	67	11 (16)	35 (52)	9 (14)	13 (19)
,,	*T. globulus*	,,	—	98	17 (17)	55 (57)	15 (15)	10 (10)
,,	*S. squamosum*	,,	—	107	18 (17)	57 (53)	17 (16)	15 (14)
,,	*N. hololeucus*	,,	165	121	14 (12)	75 (61)	15 (13)	18 (14)

Percentage of total development period for each stage given in brackets.

* Egg laid to adult emerged from its cocoon.

Obraztzov (1928) gives some information on the biology of *G. boieldieui* Levrat in houses in the Ukraine. Adults, active only in the dark, appear in March and disappear after May. Eggs are laid deep into foods, such as bread or dried butterflies, but rarely on the surface. The larva is fully fed in 3 to 5 weeks and emerges from the cocoon in September. It is not clear whether the adult then hibernates during the winter or if another generation is produced.

N. hololeucus received a great deal of attention between 1925 and 1935. Its biology in the warehouse or in uncontrolled laboratory conditions is described by Braune (1928a & b, 1929), Kemper (1935), Marcus (1929, 1930), Miles (1933), O'Farrell and Butler (1948), Pohl (1928), Pussard (1928), Reh (1929), Vogel (1929), and Zacher (1928a, b & c). Authors writing more than one paper give substantially the same information in each.

Zacher (1922) states that *N. hololeucus* originates from the Black Sea area and Voelkel (1926) that it reached London in 1837 from S. Russia.

Braune states that adults feed on animal matter, preferring dead insects. In general Ptinids breed well in dead insects but the observations of Pussard (1928) and Pohl (1928) suggest that *N. hololeucus* prefers carbohydrate and starch. In this paper it is concluded that *N. hololeucus* and also *E. hilleri* and *T. globulus* develop most quickly on starchy foods, but probably can subsist on foods entirely devoid of carbohydrate.

Adults of *N. hololeucus* may be found at any time of the year and there may be one or two generations a year. There seems to be a peak during the period August to November (see Howe, 1950 and all the papers just listed) but in some circumstances there is another emergence in the spring or early summer (Braune, Marcus, Miles, O'Farrell & Butler, Pohl, Pussard and Reh). This additional emergence must be associated with higher temperature causing quicker development ; Reh associates a winter emergence with heated buildings. The emergence dates quoted by the various authors are correspondingly late or early in the two periods mentioned. Thus Pohl states that generations appear in June to July and in October to November whilst Pussard gives April to May and August to September. O'Farrell & Butler found that *T. globulus* also was most frequently found in September to December, and had a minor peak in June.

All stages of the life-cycle occur in the warehouse together (Geinitz, 1928). Eggs may be laid at any time of year, but are especially numerous, of course, following the peaks of adult emergence. Pussard comments on the nocturnal oviposition which is typical of Ptinids not kept continuously in the dark.

Zacher (1928b) records that adults drink eagerly and Krauss (1928) and Pohl both used damp rags to trap adults. Nevertheless the importance of water for egg output has not been realised previously and when compared with the results given in this paper (Table XII), all the figures given are very low (Kemper 15 to 40, Marcus 25 to 30 and Miles 27 eggs). Similarly the lengths of adult life and oviposition period of females given in published work are often short. Thus, whereas in the work here described, some *N. hololeucus* lived and laid eggs for 150 days even at 25°C., Braune gives the adult life as being only 2 months ; Marcus also gives this period with oviposition only after the first 26 days ; Miles found that one female lived for 69 days and stopped laying after 48 days, but Vogel obtained laying for 115 days and survival for 141 days ; Zacher had adults living 158 days and Pussard 8 months.

The egg incubation period is recorded as 14 to 16 days at 20° to 22°C. (Marcus), 15 to 20 days at 19°C. (Pussard), 11 to 22 days at 16° to 20°C. (Zacher) and 26 to 30 days at 15°C. (Kemper, Pussard). In unrecorded conditions the periods given are 15 to 17 days (Braune), 17 days (Miles and Pohl). At 20°C. and 70 per cent. R.H., the mean period recorded in this paper is 14 days (Table XIV).

Both Pohl and Marcus state that larvae feed for 60 days and spend 30 days in building a cocoon ; Miles had larvae feeding for 90 days, one staying about 40 days in the cocoon and another 80 days. Zacher (1928a) had larvae only half-grown in 80 days and Pussard found the larval stage beginning in September and lasting 250 days. On wheatfeed *N. hololeucus* larvae developed in 75 days at 20°C. and 70 per cent. R.H.

For the pupal period, Marcus gives 15 to 18 days at 20°C. and 26 to 28 days at 15°C. compared with a mean of 15 days recorded here. Other records are : 14 to 22 (Kemper), 15 to 20 (Pussard), 16 to 18 (Braune), and 17 to 24 days (Miles).

Marcus found that adults remained in the cocoon for 19 to 22 days at 20°C. and 23 days in field conditions. Boldyrev (1922) gives 26 to 27 days at 11° to 15°C. and Miles 20 days for one beetle at an unspecified temperature. The mean period at 20°C. found in this paper is 18 days.

The complete life-cycle given in these papers varies from 172 days (Marcus) to 300 days (Pussard).

These papers give an accurate picture of the life of *N. hololeucus* in a warehouse except for the under-estimation of egg laying. Six months to a year is the normal adult life of Ptinids. Hickin (1941a) kept beetles of *G. psylloides* for over 30 weeks but failed to obtain many eggs probably because the adults had no access to water. At this laboratory, even when water was given, *E. hilleri* laid poorly and very few eggs have been obtained from *Tipnus unicolor* (Pill. & Mitt.) or *Ptinus villiger* Reitt.

Summary.

The biology of *N. hololeucus*, *T. globulus*, *G. psylloides*, *S. squamosum* and *E. hilleri* has been studied to estimate their potentialities as pests of stored products.

They are widely distributed and feed on a very wide range of foodstuffs of both plant and animal origin.

Adult life is usually longer than the development period. Oviposition extends over most of the adult life. In warehouses all stages of development are present together.

At 70 per cent. R.H. the developmental period (egg laid to emergence of adult from its cocoon) comprises : 12 to 21 per cent. as the egg stage, 52 to 70 per cent. as larva, 12 to 16 per cent. as pupa and 6 to 19 per cent. as adult in cocoon.

The mean lengths of the various developmental stages, including the larval instars, have been found under several sets of physical conditions.

Normally there are three larval instars, but unfavourable conditions may induce extra moults. Poor food and low humidity can cause this phenomenon.

The maximum temperature at which development is possible lies between 25° and 30°C. for all species except *G. psylloides* (35°C.) and *N. hololeucus* (25°C.). The quickest development occurs at about 33°C. for *G. psylloides*, about 25°C. for *S. squamosum*, 23° to 25°C. for *E. hilleri* and *T. globulus* and 20° to 23°C. for *N. hololeucus*. In general, beetles are heavier when bred at lower temperatures and female beetles are heavier than males.

The development of *E. hilleri* and *T. globulus* is slower and adult weight lower at 50 per cent. than at 70 per cent. R.H. The duration of the egg stage of *E. hilleri* increased from 9·9 days at 90 per cent. R.H., 10·4 at 70 per cent. and 11·7 at 50 per cent. to 16·4 days at 30 per cent. R.H. Only 30 per cent. of the eggs hatched at the lowest humidity, whereas over 70 per cent. hatched at higher humidities.

The shortest mean periods for complete development on wheatfeed, from egg laid to adult emergence from the cocoon, recorded in this paper are 45 days for *G. psylloides* at 33°C., 53 days for *E. hilleri*, 74 days for *T. globulus* and 80 days for *S. squamosum* all at 25°C. *N. hololeucus* completed development in 121 days at 20°C. but two individuals bred on wheatfeed plus yeast averaged 71·5 days at 25°C.

Of the three standard foodstuffs used, wheatfeed was the best and flour was better than fishmeal. On fishmeal, *E. hilleri* did not develop at all, but *G. psylloides* did well. In general, the difference between developmental periods on the three foods were significant statistically. The addition of yeast to wheatfeed did not improve it but addition of yeast to flour significantly reduced the development periods of *E. hilleri*, *G. psylloides* and *T. globulus*. Flour plus yeast was approximately as good as wheatfeed with or without yeast. Fishmeal was markedly improved by added yeast, but was still inferior to wheatfeed except for *S. squamosum*. The addition of yeast to fishmeal made the development of *E. hilleri* possible and reduced the mortality in all species except *G. psylloides*. Some *N. hololeucus* developed at 25°C. on wheat feed and on all three foods with yeast present. Comparison of foods with yeast added suggests that *E. hilleri*, *T. globulus* and *G. psylloides* develop better on foods of plant origin than on food of animal origin.

All species will develop on an artificial diet of casein and glucose with salts, a sterol and yeast added. The proportion of glucose and casein has little effect. The sterol is necessary, in addition to yeast, for normal speed of development. Little or no fat is necessary.

The optimum temperatures for long adult life with a large total egg output are : near 25°C. for *G. psylloides* ; below 25°C. for *T. globulus, E. hilleri* and *S. squamosum* ; and considerably below 25°C. for *N. hololeucus*. At 25°C. and 70 per cent. R.H., on wheatfeed, the mean adult life of female beetles of *G. psylloides* was between 40 and 50 weeks, of *T. globulus* 37 weeks, of *S. squamosum* 31 weeks, of *E. hilleri* 19 weeks and of *N. hololeucus* 16 weeks. At 20°C. and 70 per cent. R.H., females of *N. hololeucus* lived 23 to 24 weeks. Male beetles are shorter lived.

After the emergence of the female from the cocoon, there is a short pre-oviposition period. The rate of oviposition increases rapidly to reach a maximum, then slowly decreases as the beetle ages. At 25°C., which is optimal for egg production for *G. psylloides*, and above the optimum for the other species, the mean total egg number of *G. psylloides* was 283, of *T. globulus* 161, of *S. squamosum* 169 and of *E. hilleri* 15. Two groups of *N. hololeucus* had mean egg numbers of 16 and 46, but two females kept at 20°C. laid 81 and 223 eggs. The egg output obtained for *E. hilleri* may be low for this species. To attain their maximum egg outputs the beetles need free water to drink.

Few eggs are laid in the absence of food. When a choice of foods for oviposition was given, there were indications that the five species showed different preferences, which bore no relation to the suitability of the foods for development.

The short term effects of some foods on oviposition of *E. hilleri* have been studied. The foods which produced the best egg output were not always good foods for development, and *E. hilleri* was not especially attracted to lay on the type of food used for breeding.

The small number of natural enemies recorded in the literature for these Ptinids are listed. *N. hololeucus* and *T. globulus* are prone to disease of unknown cause, which kills many larvae and pupae and is probably transmitted in the frass.

The ability of these five Ptinids to live as general scavengers enables them to exist in empty warehouses on rat droppings and general debris.

Occasional sporadic outbreaks of *N. hololeucus* are found in storage places, but the other four species are seldom found in large enough numbers to be considered pests. In warehouse conditions, all five species, except possibly *E. hilleri*, multiply much more slowly than *P. tectus* and the present work shows that all five are unlikely to become pests.

A survey of the literature on these species has been made, particularly that on the biology of *N. hololeucus*. In storage conditions, there is an emergence of adult beetles of *N. hololeucus* between August and November. Another emergence sometimes occurs in the spring or early summer, almost certainly associated with warmer conditions. In general, the duration of the developmental stages given by various authors agree quite well with the present work, but most authors give a small egg output and short adult life, almost certainly because the importance of drinking water for the adult beetles had not been realised.

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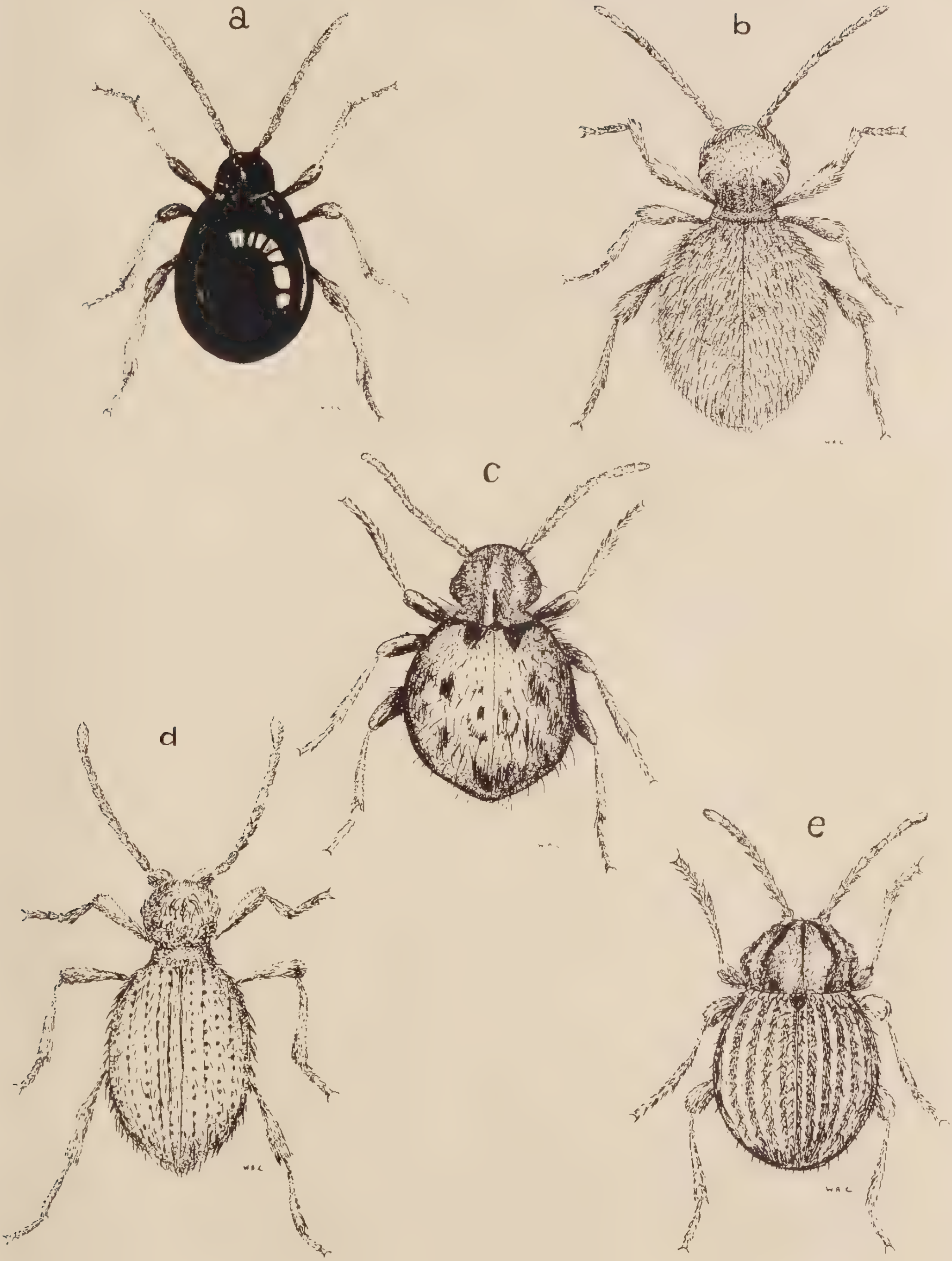
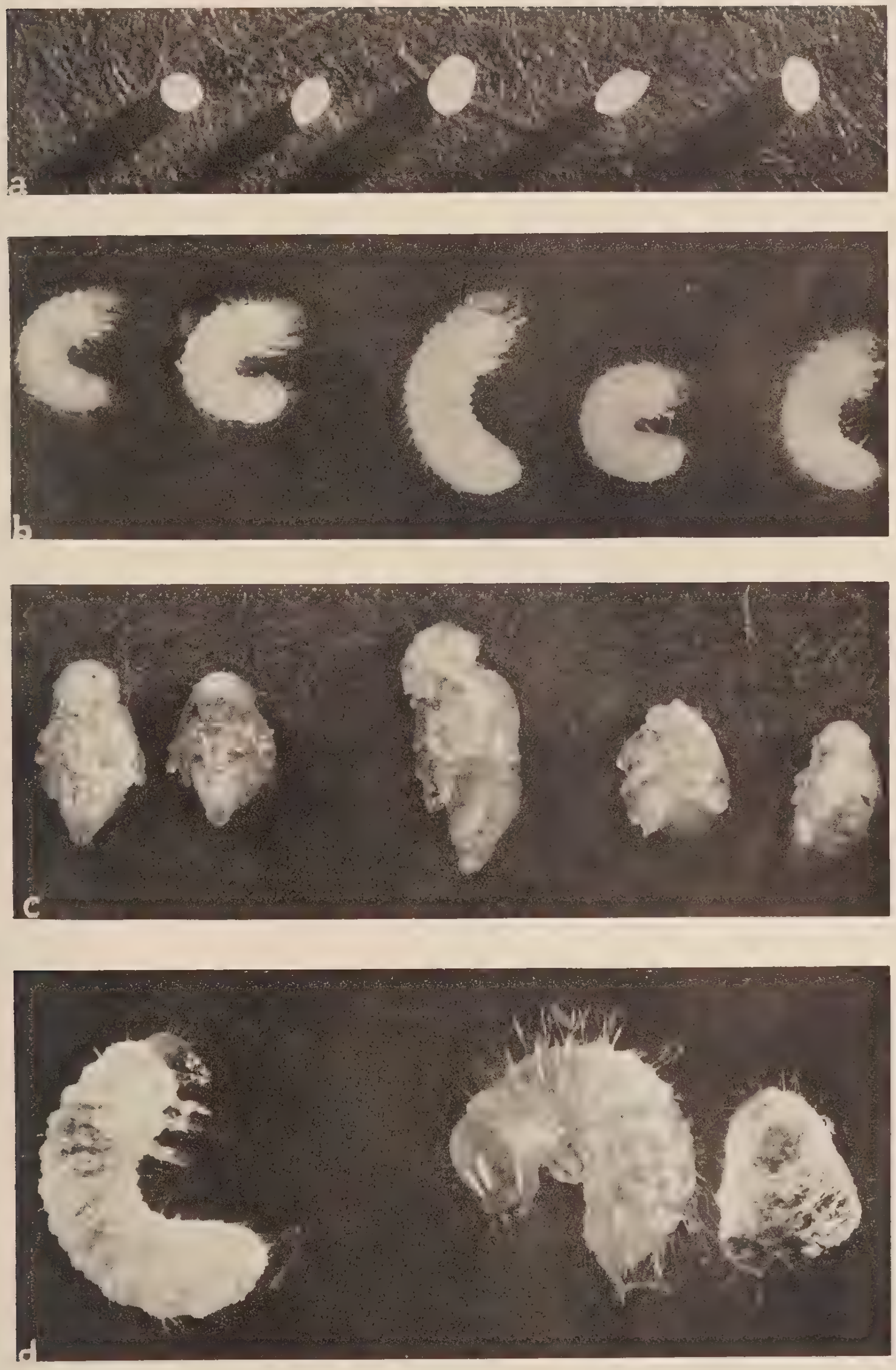


(a), *Gibbium psylloides;* (b), *Niptus hololeucus;* (c), *Trigonogenius globulus;*
(d), *Eurostus hilleri;* (e), *Stethomezium squamosum.*



Left to right: *T. globulus, S. squamosum, N. hololeucus, G. psylloides* and *E. hilleri;* (*a*), eggs; (*b*), fully fed larvae; (*c*). pupae; (*d*), larvae of *N. hololeucus;* left, first-instar larva ready to moult; right, newly moulted second-instar larva and its cast skin.

ON "SUPONA", A NEW TYPE OF DDT SUSPENSION.

By N. van Tiel.

The possibility of using modern synthetic insecticides for the control of tsetse flies has been closely investigated in the last few years.

As it is known that the effectiveness of a toxicant is influenced by the way in which it is formulated, increasing attention will have to be paid not only to the type of insecticide but still more to the type of formulation. Factors such as resistance to rain, stability towards sunlight, penetration into porous surfaces as well as the actual toxicity of the deposit depend greatly on the form in which the insecticide has been applied.

The present investigation is a contribution to the solution of some problems encountered in the control of tsetse flies, *Glossina palpalis* (R.-D.), as far as ground spraying of vegetation with products containing DDT is concerned.

Until recently there were in general three forms in which DDT could be sprayed on vegetation: as a straight solution, as a water-dispersible powder (wettable powder) and as an emulsion.

Symes, Hadaway, Barlow and Galley (1947) state that the application of DDT as a straight solution is seriously handicapped by the penetration of a considerable part of the active material into the surface of the leaves, which renders the deposits much less effective than they should be. Spraying with DDT as a water-dispersible powder does not involve this drawback, but on the other hand does not provide residues sufficiently resistant to tropical rains. Moreover, H. C. M. Parr (unpublished report, 1948) has shown that residues from dispersible powders are less stable towards tropical sunlight than residues from emulsions.

So far, DDT products of the emulsion type have given the best results.

The present investigation was carried out whilst the writer was attached to the Colonial Insecticide Research team at Entebbe, Uganda, and aimed at obtaining detailed information regarding the merits of two recently formulated DDT suspensions, "Supona"-D and "Supona"-DB, the former for the control of tsetse flies and the residual effect of both when used in African mud huts against mosquitos.

"Supona"-D and "Supona"-DB in their concentrated form are thin, creamy pastes that are easy to pour and to dilute with water. They contain about 50 per cent. DDT or 39 per cent. DDT+13 per cent. technical BHC respectively, the active material being suspended in a complex colloidal oil-water system. As the oil used has only poor solvent properties for DDT and BHC, practically all the active material is suspended as minute solid particles. When the concentrate is diluted with water, suspensions are obtained which are considerably more stable than the suspensions of the current dispersible powders. Owing to the extremely small size of the solid particles ($<25\,\mu$ in the case of DDT), there is no risk of clogging of the nozzles of the spraying machines. Moreover, residues of these suspensions are highly effective as there is no masking of the active material by inert fillers as is the case with dispersible powders.

Control of Tsetse Flies.

The effectiveness of "Supona"-D against tsetse flies, *G. palpalis*, has been examined in laboratory experiments and in field trials on a larger scale. An emulsion containing about 30 per cent. DDT dissolved in a mineral oil phase which is itself dispersed in water was used for comparison. Both products were applied in dilutions containing 5 per cent. DDT.

Laboratory experiments.

Methods.

Prior to field experiments, residues of "Supona"-D and the DDT emulsion were examined in the laboratory for toxicity, resistance to rain and stability towards tropical sunshine.

Leaves of young tea plants (*Camellia thea*) and of begonia (*Begonia* sp.) were sprayed with a dosage of about 50 mg. DDT/sq. ft. under a Potter spraying apparatus (Potter, 1941). After this the plants were left for at least 3 days to be sure that all the water of the spray on the leaves had completely evaporated, and that the residues had assumed their final structure.

The test insect used was *G. palpalis*, obtained in the laboratory from pupae collected every week on islands in Lake Victoria. After emerging, the flies were kept in wooden cages with copper gauze side walls, through which they could daily be fed on sheep.

Flies of 3 to 9 days old (rarely younger or older) that had just been fed were used for the experiments. Each leaf was tested with about ten flies, representative of all ages. For 30 seconds the flies were exposed individually to the sprayed surface in tubes of 3 × 1 ins., which were held upside down just above the surface of the leaf. The tubes were then closed with a copper gauze cap and placed in a zinc tray over some water and covered with black cloth. The activity of the DDT residues was determined from the percentage of flies paralysed after varying periods of exposure. For this purpose the knock-down values $\frac{1}{4}$, $\frac{1}{2}$, 1, 4 and 6 hours after contact with the DDT residues were ascertained. As in nearly all cases there was 100 per cent. knockdown after 4 hours, only the first three countings after exposure are of any real importance. No attention was paid to the mortality, as every paralysed fly dies after a few hours and, moreover, it is difficult to ascertain the exact moment of death.

Resistance to rain.

Six isolated tea leaves were sprayed, three with "Supona"-D and three with the DDT emulsion, at a dosage of 50 mg. DDT/sq. ft. Of each three leaves, two were exposed to artificial rain in the laboratory and one was not. The "raining" was carried out with a paint gun at a distance of only about 20 cm. from the leaf surface, in order not to lose too much of the momentum of the water drops, and at a pressure of 32 mm. mercury. The leaves were exposed three times to artificial rain with quantities of water corresponding to 11, 18 and 19 cm. of rain respectively. The activity of the residues was ascertained before and after exposure to rain on the same leaves.

It was shown that the initial toxicity of the DDT emulsion residues was higher than that of the residues of "Supona"-D. As regards resistance to rain, however, the knockdown by "Supona"-D proved in general to be less influenced by rain than that by the DDT emulsion. Both preparations, however, may be considered satisfactory in this respect. In all cases, the sprayed leaves retained a considerable part of their residual effect whether exposed to rain or not.

The results are shown in fig. 1.

This experiment was repeated with *Begonia* leaves, which are hairy and considerably thicker than tea leaves. The purpose was to ascertain whether the nature of the leaf surface had any influence on the results. It was found that the results were similar to those obtained with tea leaves. The initial toxicity of the DDT emulsion residues was higher than that of the residues of "Supona"-D. The resistance to rain of both products was satisfactory, but that of the "Supona"-D was slightly superior to that of the DDT emulsion.

A comparison was also made between the resistance to rain of a DDT emulsion (20 per cent. DDT in the concentrate) and "Supona"-D on leaves of *Prunus*

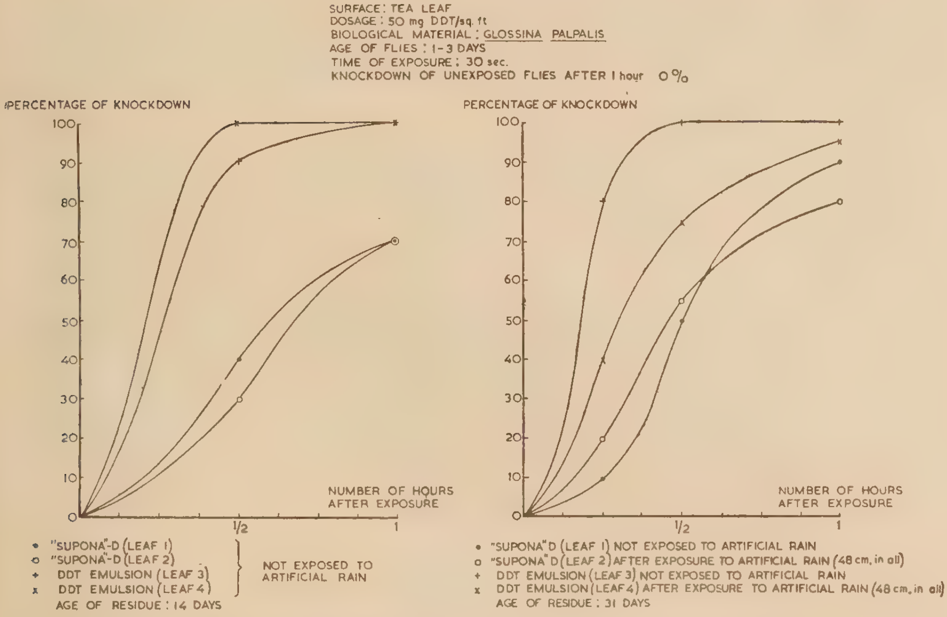


Fig. 1.—Resistance of residues from a " Supona "-D and a DDT emulsion towards artificial rain.

laurocerasus. The dosage amounted to 14 mg. DDT/sq. ft. House-flies, *Musca domestica* L., were brought for 30 sec. into contact with residues which had been exposed to artificial rain with a quantity of water corresponding to 5 cm. of rain, and with non-exposed residues. Knockdown values ½ to 4 hours after contact and 24 hours' mortality are recorded in Table I.

TABLE I.

Percentage knockdown, and mortality after 24 hours, of house-flies after contact with DDT residues on leaves of *Prunus laurocerasus* for 30 seconds.

Product	Treatment	Number of hours after contact					
		½	1	2	3	4	24
DDT emulsion ...	Not exposed to artificial rain	8	27	38	53	73	100
	Exposed to artificial rain	0	0	0	0	0	23
" Supona "-D ...	Not exposed to artificial rain	0	44	72	94	100	100
	Exposed to artificial rain	0	10	24	54	87	100
Control		0	0	0	0	0	2

It is clear from the above figures that the resistance to rain of the " Supona "-D was markedly better than that of the DDT emulsion. With the " Supona "-D there was only some decrease in knockdown values but no influence on the final mortality after artificial rain ; with the DDT emulsion, however, the artificial rain caused a drop in knockdown values to zero and in mortality from 100 to 23 per cent.

Stability towards tropical sunlight.

In addition to tropical rains, intense sunlight has an adverse influence on the activity of DDT residues on vegetation in the open. In a laboratory experiment it was ascertained to what extent the " Supona "-D and the DDT emulsion differ in this respect.

Of each of three young tea plants one leaf was sprayed with " Supona "-D, and of each of three other plants one leaf with DDT emulsion. Of each three, two were exposed to intense sunlight for 3 days (20 hours in all) while one remained unexposed. The activity of the residues was ascertained before and after exposure. It was found that the stability of the residues of " Supona "-D was lower than that of the DDT emulsion residues. The activity of the former had decreased after exposure to sunlight, whereas that of the latter had remained unchanged. The differences were not large, however, and could not be noticed in the field experiment. The results are shown in fig. 2.

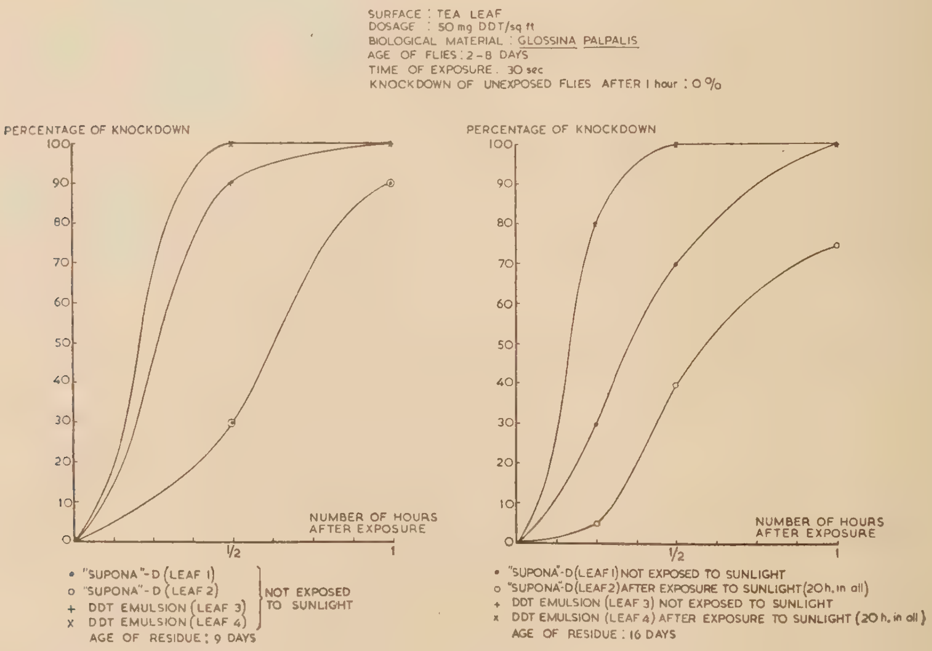


Fig. 2.—Stability of residues from a " Supona "-D and a DDT emulsion towards tropical sunlight.

Field experiments.

Two islands in Lake Victoria, Mbirubuziba and Makusu, with an area of 25 and 50 acres respectively, were selected for applications of spray to vegetation against *Glossina palpalis*. The corresponding control areas were Mbiru (peninsula) for Mbirubuziba and Sowe (island) for Makusu.

The treatment was not total but selective, *i.e.*, only those areas of the islands were sprayed where *G. palpalis* congregates by preference, *viz.*, the vegation along the paths, especially the periphery along the coast and the vegetation bordering on open spaces and clearings. The very heavy bush which covered a large part of the islands and where no tsetse flies could be expected was left untreated. The same applied to open areas without bush. The total area sprayed certainly amounted to no more than 5 to 10 per cent. of the entire island.

The islands were uninhabited and covered with abundant vegetation ; among the most frequently occurring species were *Triumfetta althaeoides* (*macrophylla*) and *Alchornea cordata*. Paths had been cut, along which there were numbered catching stations at regular intervals.

Every day (except when sprayings took place) the fly boys made a fly round : for 15 minutes at each station as many tsetse flies as possible were caught by hand with the aid of a net. The total number and the number of male flies were recorded. The average number of male flies per station over a period of 1 week (five catching days) was taken as a measure of the population density of *G. palpalis*. As on the whole the females are much less active than the males and consequently the greater part of the flies caught are males, the number of males caught gives a more reliable picture of the density than the total number of flies of the two sexes together.

The fly rounds were started 2 months before spraying took place in order to gain an idea of the normal density of *Glossina*. The treatment consisted of four applications of spray at fortnightly intervals, in order to be sure of controlling at least two complete generations. The sprays used were 5 per cent. DDT containing dilutions of " Supona "-D (Makusu) and DDT emulsion (Mbirubuziba).*

Fly rounds were continued after treatment to ascertain the residual effect and the persistency of the effect of the two products under the influence of sunlight and rain.

The vegetation was sprayed up to a height of about 7 ft., as well as the soil below shrubs, tree trunks, etc., where the pupal sites occur. The sprays were applied with Four Oaks knapsack sprayers. The two products had excellent spraying properties.

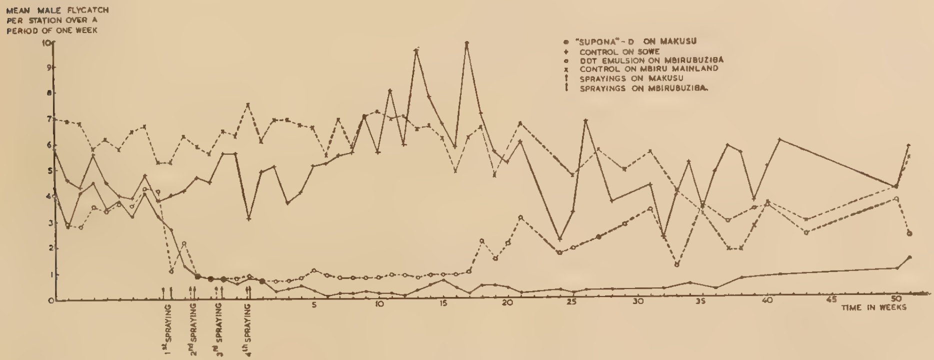


Fig. 3.—Reduction and recovery of tsetse fly population after vegetation spraying with " Supona "-D and DDT emulsion on Islands in Lake Victoria.

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* As the supply of the original DDT emulsion was insufficient for all four sprayings, half of the entire treatment was done with a 5 per cent. DDT dilution of a related emulsion, containing about 25 per cent. of DDT dissolved in a mineral oil which is itself dispersed in water.

Fig. 3 gives a survey of the fly catches before and after spraying (four treatments in all) on Mbirubuziba and Makusu as compared with the control areas Mbiru mainland and Sowe.

The average catch of male flies per station in a week amounted to 3·6 during the 2 months before the spray was applied, both on Mbirubuziba and on Makusu. During that time it varied from 2·8 to 4·3 on Mbirubuziba and from 2·7 to 4·5 on Makusu.

Immediately after the first application of spray these numbers dropped from 4·3 (last catch before treatment) to 1·1 on Mbirubuziba (DDT emulsion) and from 2·9 (last catch before treatment) to 1·3 on Makusu (" Supona "-D). Although the drop was less pronounced with the " Supona "-D than with the DDT emulsion—which is in agreement with the higher initial toxicity of the DDT emulsion residues found in the laboratory—it must be borne in mind that the catch just before the spraying was low on Makusu and high on Mbirubuziba.

During the period of the second, third and fourth treatments the catches on both islands amounted to an average of 0·8, *i.e.*, the tsetse fly population had dropped to 22 per cent. of the original.

A fortnight after the last treatments, notwithstanding the frequent rains, there was a further drop on Makusu (" Supona "-D), so that 6 weeks after the last spraying the tsetse fly population had been reduced to 3 per cent. of the original ; after that the population remained constant for at least another 6 weeks at an average of 6 per cent. as compared with that before the treatment.

When surveying the course of the tsetse population on Makusu for the next 39 weeks (total period after last treatment : 51 weeks), it was clear that there was only a very slight upward tendency. Not until 36 weeks after spraying did a definite continuous increase in catches set in, reaching a level of 39 per cent. of the pre-spraying values 51 weeks after the last spraying.

On Mbirubuziba (DDT emulsion), however, the situation was different. For a period of 17 weeks after the last treatment the population remained practically constant at 22 per cent. of the original figure. Then, coinciding with a period of heavy rains, a sudden increase set in, which continued with ups and downs until 35 weeks after the last treatment when the catches regained their pre-spraying values.

Chemical analyses of leaf samples (*Alchornea cordata*) taken 4 weeks after the last application of spray showed deposits of 87 mg. DDT /sq. ft. on Mbirubuziba and of 79 mg. DDT /sq. ft. on Makusu. Further analyses 22 weeks after the last treatment however, showed no DDT on Mbirubuziba and only slight amounts on Makusu.

Both the biological and the chemical data point to a better persistency under field conditions of the " Supona "-D as compared with the DDT emulsion used. As far as resistance to rain is concerned, this is in agreement with the results of the laboratory experiments, especially with those given in Table I.

Summarising the results of the field experiment it may be said that both " Supona "-D and DDT emulsion were active as vegetation sprays against tsetse flies. Over a prolonged period " Supona "-D gave the more effective and persistent residues and may be recommended if ground spraying on vegetation against *G. palpalis* has to be carried out.

Application to Mud Huts against Mosquitos.

Two methods may be adopted for the control of mosquitos :—

1. The surface of the water in which the mosquitos breed may be sprayed with insecticidal solutions (preferably DDT solutions in oil) in order to kill the *Anopheles* larvae.

2. Walls and roofs of the houses inside may be sprayed in order to kill the adult Anophelines (residual sprays).

Local circumstances determine which of the two methods will be the most economic in actual application. The present investigation deals only with the effect of residual sprays in African mud huts. Many experiments have been carried out in this field particularly with DDT solutions in kerosene and DDT dispersible powders. Both preparations have considerable drawbacks, however, for DDT solutions penetrate very quickly into the extremely porous walls of mud huts, as a result of which more than 50 per cent. of the active material is often lost.

In the case of dispersible powder suspensions, the active material does not penetrate into the mud. These preparations have a low stability in suspension, and consequently the DDT soon settles at the bottom of the tank or knapsack sprayer, with the result that the quantity of DDT in the sprayed liquid is reduced.

The effectiveness of "Supona"-D and "Supona"-DB against mosquitos has been examined both in the laboratory and in field trials. A commercial dispersible powder (Guesarol 33) containing 33 per cent. of DDT was used for comparison.

Laboratory experiments.

Before starting field trials, the toxicity of residues of "Supona"-D was compared with that of DDT dispersible powder.

Little blocks of mud were sprayed with "Supona"-D and DDT dispersible powder diluted to a 5 per cent. DDT content at a dosage of about 50 mg. DDT/sq. ft. under a Potter spraying apparatus. Tsetse flies, *G. palpalis*, were used as test insects as they were readily available. They were individually exposed for 30 sec. to the toxic residue as described above (p. 188). The results are given in fig. 4 and show that residues of "Supona"-D were more toxic than those of DDT dispersible powder.

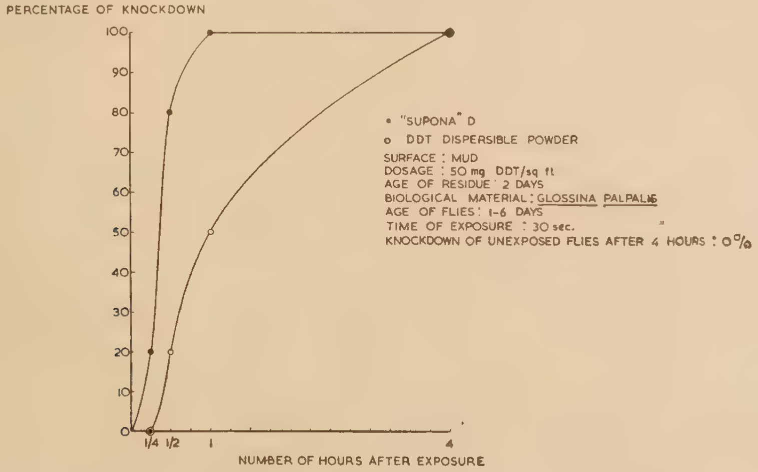

Fig. 4.—Initial toxicity of residues from "Supona"-D and DDT dispersible powder on mud.

In order to determine to what percentage the DDT in the diluted "Supona"-D could be reduced to obtain the same activity as the DDT dispersible powder, mud blocks were sprayed with "Supona"-D containing 5 per cent., 4 per cent., 3 per cent., 2 per cent. and 1 per cent. DDT giving dosages of 50, 40, 30, 20 and 10 mg. DDT/sq. ft., respectively, and with a 5 per cent. DDT-containing dispersible powder suspension at a dosage of 50 mg. DDT/sq. ft. The results are summarised in fig. 5.

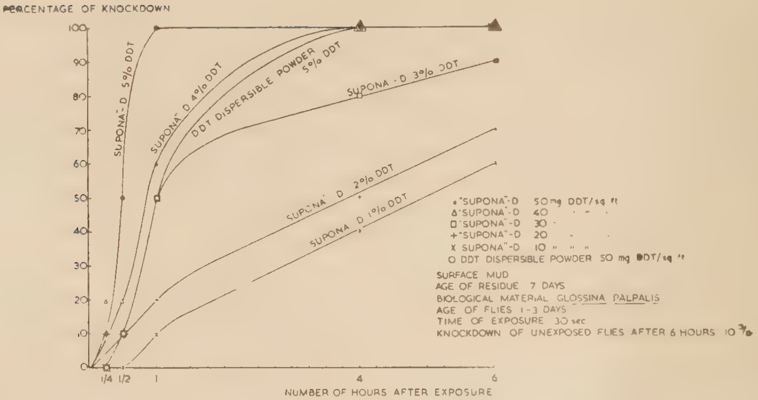

Fig. 5.—Initial toxicity of residues from DDT dispersible powder as compared with "Supona"-D at various dosages on mud.

It is clear from the above figure that residues of "Supona"-D at 10 and 20 mg. DDT/sq. ft. are decidedly lower in toxicity than those of DDT dispersible powder at 50 mg. DDT/sq. ft. Residues of "Supona"-D at 30 mg. DDT/sq. ft. were only slightly less toxic than the latter in this experiment. A repetition of these tests showed that residues of "Supona"-D at 30 mg. DDT/sq. ft. were sometimes equally toxic, sometimes slightly more or less toxic than DDT dispersible powder residues at 50 mg. DDT/sq. ft. Residues of "Supona"-D at 40 and 50 mg. DDT/sq. ft., however, were in all cases markedly more toxic.

From these experiments it may be concluded that the DDT content in diluted "Supona"-D can, at all events, be reduced from 5 per cent. to 4 per cent. and yet retain a toxic effect corresponding with that of a 5 per cent. DDT-containing dilution of the dispersible powder used in these experiments.

Field trials.

Small-scale trial at Mpala.

The merits of "Supona"-D as a residual spray against mosquitos compared with DDT dispersible powder have been examined in a small-scale trial at Mpala (near Entebbe).

The experimental lay-out consisted of three native mud huts and three wooden experimental huts built for the experiment.

The mud huts were simple round huts, with thatched roofs, fitted with a window to which an exit trap of mosquito netting was fixed. The door was kept open during the night and the entrance covered by means of a loose black cloth, so that the mosquitos could enter via the chinks. To attract the mosquitos, people slept in the huts during the nights preceding the early morning catches. When the catches were being made in the early morning, the door was closed to prevent the flying mosquitos from escaping. A small cemented trench filled with oil-covered water was constructed round the mud huts in order to prevent ants coming in during the night and destroying the paralysed mosquitos.

The wooden experimental huts were fitted with two entry traps (through which the mosquitos could easily fly into the hut, but through which they could only leave with difficulty) and an exit trap (in which the out-flying mosquitos were collected and from which they could hardly enter the hut again). The wooden huts too were slept in during the night preceding the early morning catches.

The wooden huts were on wooden poles greased in order to exclude ants.

All the experimental huts were checked twice a week in the early morning (about 6.30 a.m.) ; live and dead female mosquitos, *Anopheles gambiae* Giles, *A. funestus* Giles and Culicines, in the huts and in the exit traps were collected by hand and identified. To facilitate the finding of dead mosquitos, the floors were covered with white sheets on the previous night.

The huts were treated as follows :—

1 mud hut ...	"Supona"-D	roof 100 mg. DDT/sq. ft.	wall 50 mg. DDT/sq. ft.
1 mud hut ...	DDT dispersible powder	roof 100 mg. DDT/sq. ft.	wall 50 mg. DDT/sq. ft.
1 mud hut ...	untreated		
1 wooden hut	"Supona"-D	175 mg. DDT/sq. ft.	
1 wooden hut	DDT dispersible powder	175 mg. DDT/sq. ft.	
1 wooden hut	untreated		

The sprays were applied by means of a Four Oaks knapsack sprayer. During treatment, sample papers were attached at random to the wall and the roof and afterwards analysed chemically for DDT. The average dosages actually found are given above.

TABLE II.

Mosquito catches in wooden experimental huts.

Product	Species		Before spraying		After spraying									Total number after spraying	Total percentages after spraying
"Supona"-D	*Anopheles gambiae* ♀	alive	8	15	0	.0	0	0	0	0	0	0	0	0	0
		killed	0	0	10	5	4	2	2	6	10	3	2	44	100
	Anopheles funestus ♀	alive	54	25	0	0	0	0	0	0	0	1	0	1	2
		killed	0	0	6	3	3	4	2	8	10	8	1	45	98
	Culicines ♀	alive	—	38	0	0	1	0	0	0	2	5	0	8	4
		killed	—	0	14	20	29	4	10	13	38	47	8	183	96
DDT dispersible powder	*Anopheles gambiae* ♀	alive	0	15	0	0	0	0	0	0	0	0	0	0	0
		killed	0	0	11	7	9	5	3	3	4	1	0	43	100
	Anopheles funestus ♀	alive	33	46	0	0	0	0	0	0	0	0	0	0	0
		killed	0	0	10	5	4	2	3	2	2	0	1	29	100
	Culicines ♀	alive	—	63	0	1	1	1	1	2	4	1	4	15	11
		killed	—	0	16	30	23	12	7	6	15	11	3	123	89
Control	*Anopheles gambiae* ♀	alive	9	11	20	9	10	8	21	17	21	9	4	119	100
		killed	0	0	0	0	0	0	0	0	0	0	0	0	0
	Anopheles funestus ♀	alive	70	42	17	10	7	7	20	18	22	15	2	118	99
		killed	0	0	0	0	0	0	0	0	0	1	0	1	1
	Culicines ♀	alive	—	58	32	46	45	11	21	18	29	25	9	236	99·5
		killed	—	0	0	0	0	0	0	0	0	1	0	1	0·5

Each figure represents the sum of six catches over a period of three weeks.

The results of the inspections for 6 weeks before and 6 months after spraying are given in detail in Tables II and III.

As is seen from these tables, no live *A. gambiae* or *A. funestus* were found either in the wooden huts or in the exit traps for 5 months after spraying the huts with the two preparations, and only one specimen of *A. funestus* was found in the "Supona"-D treated hut 6 months after treatment. Some live Culicines were found during this period, but the percentage was only 4 per cent. after spraying with "Supona"-D and 11 per cent. after spraying with DDT dispersible powder.

The catches in the mud huts yielded similar results. No live *A. gambiae* or *A. funestus* were found for six months after spraying with "Supona"-D either in the hut or in the exit trap. Live Anophelines were not found in the exit trap until four months after spraying with DDT dispersible powder, viz. 4 *A. gambiae* and 6 *A. funestus*. Over a period of six months, the number of live Anophelines (*A. gambiae* and *A. funestus* together) was 0 per cent. after spraying with "Supona"-D and 14 per cent. after spraying with DDT dispersible powder. For the Culicines the percentages over the same period were 6 per cent. with both preparations.

TABLE III.

Mosquito catches in experimental mud huts.

Product	Species		Before spraying		After spraying									Total number after spraying	Total percentages after spraying
"Supona"-D	*Anopheles gambiae* ♀	alive	1	2	0	0	0	0	0	0	0	0	0	0	0
		killed	0	0	5	8	1	9	2	14	8	3	2	52	100
	Anopheles funestus ♀	alive	27	8	0	0	0	0	0	0	0	0	0	0	0
		killed	0	0	7	7	1	2	4	8	16	6	1	52	100
	Culicines ♀	alive	—	13	0	0	0	0	0	1	7	2	0	10	6
		killed	—	0	13	19	13	6	3	10	45	38	7	149	94
DDT dispersible powder	*Anopheles gambiae* ♀	alive	2	4	0	0	0	0	0	4	0	0	0	4	12
		killed	0	0	4	0	15	0	0	6	3	2	0	30	88
	Anopheles funestus ♀	alive	15	12	0	0	0	0	0	6	0	0	0	6	16
		killed	0	0	3	4	1	3	0	9	6	4	1	31	84
	Culicines ♀	alive	—	11	0	0	1	0	0	3	0	2	0	6	6
		killed	—	0	10	18	23	12	6	8	14	5	4	100	94
Control ...	*Anopheles gambiae* ♀	alive	3	5	4	5	6	4	4	5	1	3	0	32	100
		killed	0	0	0	0	0	0	0	0	0	0	0	0	0
	Anopheles funestus ♀	alive	32	18	20	8	7	6	3	13	5	9	0	71	95
		killed	0	0	0	0	0	0	0	0	0	4	0	4	5
	Culicines ♀	alive	—	7	12	16	28	2	5	6	12	19	0	100	86
		killed	—	0	0	0	0	0	0	0	0	16	0	16	14

Each figure represents the sum of six catches over a period of three weeks.

The results of the Mpala experiment show that DDT was 100 per cent. effective against both *A. gambiae* and *A. funestus* for at least four months after spraying. Culicines proved to be in general somewhat more resistant than Anophelines. Over a period of half a year after spraying, the "Supona"-D was on the whole more effective than the DDT dispersible powder.

Mud hut sprayings at Kisubi.

The small scale trial at Mpala was made under more or less standardised conditions. An experiment under normal conditions on a larger scale was carried out in the Kisubi mission area (near Kampala), which was badly infested with mosquitos.

The purpose of this trial was to ascertain whether there might be any appreciable differences in the persistency of the residual effect of different products, *viz.* "Supona"-D and "Supona"-DB and DDT dispersible powder.

Of the numerous native mud huts in the Kisubi area, 30 were selected for the experiment. The mosquito infestation was measured by means of early morning catches made as follows: sheets of white cloth were laid on the floor inside the huts and the live mosquitos were knocked down by means of a pyrethrum space spray (which has practically no residual effect). Mosquitos were collected on the sheets and identified afterwards, and the numbers of male and female *A. gambiae*, *A. funestus* and Culicines in general were recorded.

Each of the experimental huts was inspected once a week for a period of three weeks before and of four weeks after treatment. After that, inspections were made once a fortnight. The treatment consisted of one residual spraying of each hut by means of a Four Oaks knapsack sprayer.

Mud huts sprayed with each of the three preparations mentioned above were scattered over the whole experimental area amongst other untreated huts in order to avoid local influences on the effect of any of these products.

Five sample papers were placed at random on the walls of each hut for subsequent chemical estimation of the DDT deposited during the actual spraying. Only relatively low dosages were applied in order to enable the population to build up again in some measure within a reasonable period and thus permit a comparison of the residual effects to be made. The details of the treatments are shown in Table IV.

TABLE IV.

Mud hut sprayings against mosquitos at Kisubi.

Number of mud huts	Product	Percentage of active material in diluted spray liquid	Mean dosage on sample papers
7	"Supona"-DB* ...	0·75 per cent. DDT + 0·25 per cent. BHC	53 mg. DDT+18 mg. BHC/sq. ft.
7	"Supona"-D	0·6 per cent. DDT	116 mg. DDT/sq. ft.
8	DDT Dispersible powder	1 per cent. DDT	104 mg. DDT/sq. ft.
8	Control (unsprayed) ...		

*Technical BHC containing 14 per cent. γ-isomer.

The records of the catches before and after spraying are summarised in Table V. Each figure represents the sum of three catches in 7 or 8 huts together.

The catches before treatment give an indication of the normal mosquito population in the Kisubi area. *A. funestus* are more numerous than *A. gambiae* and, as compared with the Culicines, Anophelines are in the majority. Some male

Anophelines follow the females into the native mud huts but only a very few male Culicines were found inside the huts.

For a more exact appreciation of the effect of the treatments it is necessary to express the number of live mosquitos as percentages calculated on the expected populations (if no treatment had taken place), based on the fluctuations in population found in the untreated huts in the corresponding weeks. This is done in the last column of Table V. The corrected percentages are plotted in fig. 6.

Fig. 6 shows that the first drop in mosquito catches after treatment was about the same for all three products and amounted to 98 or 99 per cent. For the first 12 weeks after treatment, the catches were somewhat higher in the DDT dispersible powder treated huts ; then a more rapid increase set in, showing an approximately equal residual effect of " Supona "-D and DDT dispersible powder and recovery to about 30 per cent. of the original population, 29 weeks after spraying. The best results were obtained with " Supona "-DB giving a recovery of only 8 per cent. 29 weeks after spraying, notwithstanding the total dosage in the DDT-BHC treated huts (as shown by the sample papers) being less than in the DDT treated huts. These findings suggest that a combination of DDT and BHC may be preferable to DDT alone in the control of mosquitos by means of residual spraying.

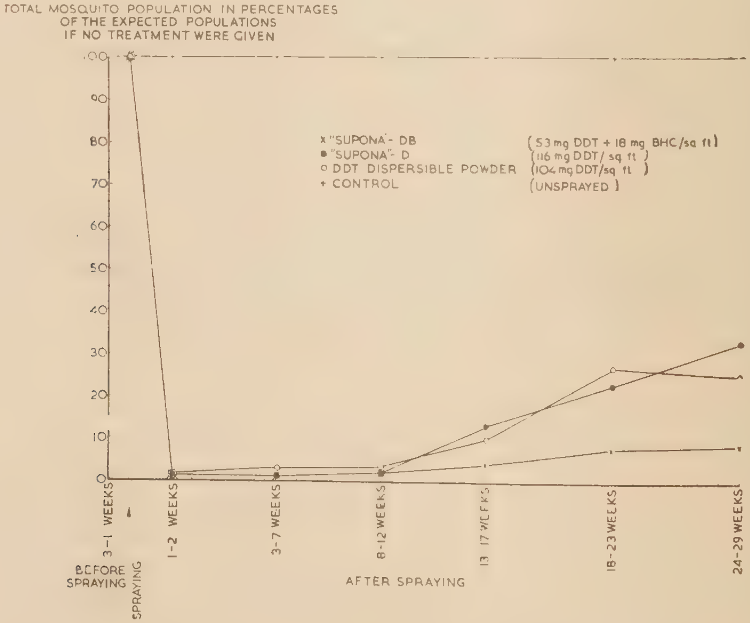

Fig. 6.—Effect of residual spraying on the mosquito population in mud huts.

A comparison of the results of the Kisubi experiment with those of the Mpala trial reveals that a complete eradication for four months was obtained at Mpala, whereas in the Kisubi huts some living mosquitos were still found immediately after spraying. It should be stressed, however, that the treatments at Mpala were carefully applied in experimental huts under more or less standardised conditions. The Kisubi sprayings were carried out under normal conditions in inhabited mud huts, the treatment of which was considerably more difficult. It may be interesting to compare the results of the Mpala and Kisubi trials with those obtained by Muirhead

TABLE V.

Mosquito catches in the Kisubi mud huts.

Product	Date	*A. gambiae*			*A. funestus*			Culicines			Total number of mosquitos	Total percentages of mosquitos	Total percentages of mosquitos (corrected)
		females	males	total	females	males	total	females	males	total			
	3-1 weeks before spraying	136	55	191	169	78	247	221	0	221	659	100	100
" Supona "-DB	1–2 weeks	0	2	2	0	0	0	4	0	4	6	0·9	1·2
	3–7 weeks	0	0	0	0	3	3	2	0	2	5	0·8	1·0
	8–12 weeks after	2	0	2	3	1	4	9	0	9	15	2·3	2·0
	13–17 weeks spraying	12	2	14	11	3	14	13	1	14	42	6·4	4·6
	18–23 weeks	28	9	37	14	2	16	26	1	27	80	12·1	8·1
	24–29 weeks	11	4	15	14	3	17	13	0	13	45	6·8	9·4
	3–1 weeks before spraying	75	26	101	178	48	226	115	0	115	442	100	100
" Supona "-D	1–2 weeks	1	1	2	1	0	1	2	0	2	5	1·1	1·4
	3–7 weeks	3	0	3	1	0	1	0	0	0	4	0·9	1·1
	8–12 weeks after	4	0	4	0	4	4	3	0	3	11	2·5	2·2
	13–17 weeks spraying	22	11	33	16	9	25	22	0	22	80	18·1	13·1
	18–23 weeks	74	9	83	28	3	31	40	0	40	154	34·8	23·2
	24–29 weeks	60	11	71	14	4	18	18	0	18	107	24·2	33·5
	3–1 weeks before spraying	113	34	147	183	59	242	194	0	194	583	100	10
DDT dispersible powder	1–2 weeks	0	3	3	1	0	1	3	0	3	7	1·2	1·7
	3–7 weeks	1	2	3	4	4	8	2	0	2	13	2·2	2·7
	8–12 weeks after	5	3	8	3	5	8	7	0	7	23	3·9	3·4
	13–17 weeks spraying	28	6	34	10	7	17	25	1	26	77	13·2	9·5
	18–23 weeks	121	32	153	33	4	37	49	1	50	240	41·2	27·4
	24–29 weeks	38	10	48	17	3	20	38	0	38	106	18·2	25·2
	3–1 weeks before spraying	69	38	107	138	85	223	675	0	675	1,005	100	100
Untreated	1–2 weeks	60	21	81	116	34	150	496	0	496	727	72·3	100
	3–7 weeks	47	25	72	107	69	176	557	0	557	805	80·1	100
	8–12 weeks after	157	38	195	246	99	345	626	0	626	1,166	116·2	100
	13–17 weeks spraying	355	86	441	199	43	242	681	26	707	1,390	138·3	100
	18–23 weeks date	418	79	497	246	92	338	655	16	671	1,506	149·9	100
	24–29 weeks	106	12	118	195	54	249	355	3	358	725	72·1	100

Thomson (1947, 1949). According to Muirhead Thomson, DDT residues are insufficiently effective against *A. gambiae*, whereas with BHC an adequate control can be obtained.

The results of the Mpala sprayings showed that the first statement of Muirhead Thomson could not be confirmed. The better control obtained at Kisubi with " Supona "-DB as compared with " Supona "-D, however, supported his statement that BHC should be more effective than DDT. Another explanation of the superior effect of " Supona "-DB may be found in a possible synergistic action of DDT and BHC in combined sprays, as has been recently stated by Rajindar Pal (1951).

Further experiments on a larger scale should be designed to ascertain whether BHC or DDT, or a combination, is the best residual spray against mosquitos in general and *A. gambiae* in particular and whether the volatility of BHC affects the persistency over a more prolonged period.

Summary.

The properties of two DDT suspensions of a new type, " Supona "-D and " Supona "-DB are described. These suspensions contain about 50 per cent. DDT or 39 per cent. DDT + 13 per cent. technical BHC respectively in their concentrated forms, the active material being suspended in a complex colloidal oil-water system.

Experiments were carried out with " Supona "-D and a DDT emulsion containing about 30 per cent. DDT dissolved in a mineral oil phase for the control of *Glossina palpalis*. Both products were applied in dilutions containing 5 per cent. DDT.

Laboratory experiments with leaves of *Camellia thea* and *Begonia* sp. showed that the initial toxicity and stability in tropical sunlight of residues of " Supona "-D were somewhat less than those of the DDT emulsion. The resistance to rain, however, was better with residues of " Supona "-D.

Two islands in Lake Victoria were given four applications of spray at fortnightly intervals, the one with " Supona "-D, the other with DDT emulsion. Only those parts of the vegetation normally inhabited by tsetse flies were treated and this comprised about 5 to 10 per cent. of the total area.

The DDT emulsion gave a rapid reduction of the tsetse fly population to 22 per cent. of the original density and that reduction was maintained for 17 weeks after the last treatment. Then a marked increase set in, coinciding with a period of heavy rains, until 35 weeks after the last treatment the population density was the same as before treatment.

" Supona "-D also gave an immediate reduction to 22 per cent. of the original population but a fortnight after the last treatment there was a further reduction to 3 per cent. ; after this the population remained constant for at least 6 weeks at a level of 6 per cent. There was only a very slight upward tendency up to 36 weeks after the last treatment and the catches remained very low. A more definite continous increase then set in until a level of 39 per cent. of the original density figure was reached 51 weeks after the last treatment.

Chemical analyses of leaf samples showed about equal amounts of DDT 4 weeks after the last application of spray in respect of both formulations but 22 weeks after treatment no DDT was present in the case of the emulsion and only very slight amounts in that of " Supona "-D.

The results of these experiments suggest that residues of " Supona "-D have a more lasting effect on vegetation than those of the DDT emulsion with which it was compared.

Experiments were also carried out with "Supona"-D as a residual spray against mosquitos.

Laboratory experiments showed that residues of "Supona"-D at 50 mg. DDT/sq. ft. on mud surfaces are more toxic than corresponding residues of DDT dispersible powder. The DDT content in the diluted "Supona"-D could be reduced from 5 per cent. to 4 per cent. and yet give the same residual toxicity as with a dilution of dispersible powder containing 5 per cent. DDT.

A small experiment was carried out to compare "Supona"-D as a residual spray with DDT dispersible powder using three experimental mud huts and three wooden experimental huts. In the case of the former the roofs were sprayed to give a deposit of 100 mg. DDT/sq. ft. and the walls 50 mg. DDT/sq. ft., in the latter a deposit of 175 mg. DDT/sq. ft. The results over a period of six months after treatment showed that "Supona"-D was on the whole more effective than the DDT dispersible powder. The DDT dispersible powder, however, was 100 per cent. effective for at least four months after treatment against both *Anopheles gambiae* and *A. funestus*. Culicines proved to be somewhat more resistant than Anophelines to both treatments.

A larger scale experiment was carried out in the Kisubi mission area on thirty native mud huts using "Supona"-DB, "Supona"-D and a DDT dispersible powder. The mean dosages on sample papers were respectively 53 mg. DDT+18 mg. BHC/sq. ft., 116 mg. DDT/sq. ft. and 104 mg. DDT/sq. ft. After treatment the number of live mosquitos per hut dropped to between 1 and 2 per cent. of the original value. This was followed by a gradual increase during the next 12 weeks which was rather more pronounced in the case of the DDT dispersible powder. Catches over a period of 29 weeks showed no significant difference in the persistency of "Supona"-D and DDT dispersible powder. The best results were obtained with "Supona"-DB in which the recovery was only 8 per cent. 29 weeks after treatment.

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THE ARTHROPOD POPULATION OF THE SOIL IN SOME EAST AFRICAN PASTURES.

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As part of our contribution to the wireworm survey of England and Wales in 1939–42, Dr. F. S. J. Hollick and I developed a new method of extracting wireworms and other insects from the soil (Salt & Hollick, 1944). When the urgency of the wireworm work slackened off, the method was applied to a study of the whole arthropod fauna of pasture soil, and revealed the presence in an English pasture of a population of soil arthropods greatly in excess of the generally accepted numbers. Recent summaries (*e.g.*, Brues, 1946, pp. 21–22 ; Allee & others, 1949, p. 473) record estimates which lie in the order of 3½ to 5 million insects per acre of grassland, or about 900 per square metre. Our studies of an ordinary pasture near Cambridge disclosed a population of insects a hundred times greater than this, and showed that terrestrial arthropods as a whole, insects and arachnoids together, could occur in English grassland soil at a rate of over 1,068 millions per acre, or 263 thousands per square metre (Salt & others, 1948).

It was clearly desirable to compare these observations of an English pasture with conditions in other parts of the world, and the possibility of visiting East Africa in order to study the arthropod fauna of tropical soils was therefore considered. Through the kind offices of Dr. H. H. Storey, C.M.G., F.R.S., a research scheme was established by the Colonial Office with the aid of the Colonial Development and Welfare Research Funds ; and the project was placed under the general scientific direction of Dr. B. A. Keen, F.R.S., Director of the East African Agriculture and Forestry Research Organization. Under these auspices, I was able to spend nine months, from July 1948 to April 1949, in East Africa.

Preliminary tours in Kenya, Tanganyika and Uganda were arranged by Dr. Keen, in order that a variety of soils and crops might be rapidly surveyed and places suitable for detailed work might be selected. Laboratory accommodation was available at only a few centres and it was decided to concentrate the soil studies at two of them, the Coffee Research Station, Lyamungu, Tanganyika, and the Agricultural Research Station, Kawanda, Uganda. The situation of Lyamungu on the lower slopes of Kilimanjaro allowed samples of one type of soil, Kilimanjaro Lava Soil, to be examined from a wide range of altitudes associated with diverse conditions of rainfall and temperature. At Kawanda there were available for examination the soils of the Buganda Catena, which are of wide extent and great importance in the Protectorate.

At both centres the principal object of the work was to obtain quantitative information about the arthropods inhabiting East African soil. The information collected for that purpose is set out in this paper, and is used as the basis for a preliminary comparison of the arthropod population of temperate and tropical soils. At Kawanda, where important research was in progress on the effects of elephant grass on soil, an additional project was undertaken, namely, to investigate the soil fauna under that grass in the hope of contributing to the wider research. The information collected on that subject will be reported in another paper.

It must be emphasized that the investigation was exploratory in nature. In a completely equipped laboratory at Cambridge it required 3·3 man-days to remove and roughly classify the entire arthropod fauna from each soil sample. Under the conditions found in Africa, the rate of work was a good deal slower. It follows that few soil samples could be thoroughly studied in the time available. In view of the large sampling errors inseparable from work on populations of soil arthropods, great care must be taken when attempting to draw conclusions from scanty information. I regard the following observations as serving the purposes merely of a preliminary survey. Much more extended studies are needed before we can claim to have more than a smattering of knowledge of the arthropod population of tropical soil.

Methods.

A full account of the method developed by us to extract arthropods from soil is to be written by Dr. Hollick, but is unfortunately not yet available. A preliminary account of it, as it was used for research on wireworms, has already been published (Salt & Hollick, 1944) but it seems desirable to describe the various processes here so as to make the method available for use or for criticism to readers of this paper. The technical problem to be solved in collecting the arthropods from a soil sample can be conveniently considered in four parts: (1) breaking the lumps of soil so as to release any animals they may contain; (2) freeing the animals from roots in which they may be entangled; (3) removing the animals from the mineral soil; (4) separating the arthropods from all other material, animal or vegetable, collected with them.

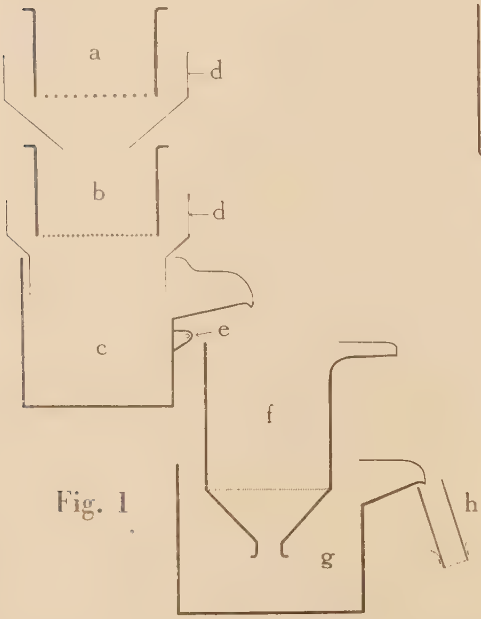

Fig. 1

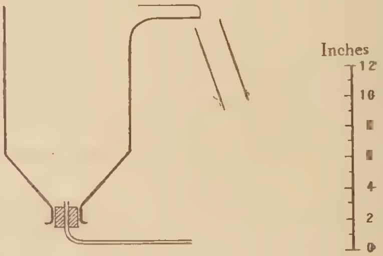

Fig. 2

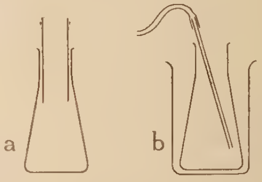

Fig. 3

Fig. 1.—Arrangement of apparatus for sieving: *a*, first sieve; *b*, second sieve; *e*, reservoir; *d*, *d*, spash guards; *e*, pivot about which reservoir is tilted; *f*, fourth (flotation) vessel; *g*, tank; *h*, bolting-silk sieve.

Fig. 2.—Arrangement of apparatus for flotation.

Fig. 3.—Apparatus used for separation of arthropods from vegetation: *a*, flask receiving material from glass cylinder; *b*, arrangement for overflow of material from the benzene layer.

(1) *Breaking the lumps of soil.*

It is necessary to break down lumps of soil in order to make sure that no animals are confined within them. The method adopted for this purpose depends on freezing. Each soil sample is brought from the field in a small tin box, 7½×6×6 in. On arrival at the laboratory, enough water is poured into the tin to cover the soil it contains, and the sample is put at a temperature of −12°C. After refrigeration for forty-eight hours, or as much longer as may be convenient, the tin is put at room temperature and in about twenty-four hours the sample has thawed and is ready for further treatment.

The soil is now washed under jets of water through two wire sieves (fig. 1, *a* and *b*) into a reservoir (fig. 1, *c*). The three vessels are arranged on a metal stand fitted with sloping guards (fig. 1, *d*, *d*) to catch and return any splashes. The two sieves have square meshes, 7 and 2·5 mm. across respectively. Even heavy clay soils are so disintegrated by the freezing that, under the action of the water, they readily pass through both sieves. In short, the soil has been broken up so that no lumps remain of a diameter larger than 2·5 mm., and in practice it is found that the soil has disintegrated into its constituent particles.

(2) *Freeing the animals from vegetation.*

When all the soil has been washed through the two sieves there may remain long roots and large pieces of vegetable matter retained by the 7 mm. sieve, and shorter roots, small mollusc shells, and other debris in the 2·5 mm. sieve. The long roots in the upper sieve are now pulled apart and washed under so strong a jet of water that no animal can remain entangled by them. Then, after visual examination, they are discarded. The upper sieve and its guard can now be lifted out of the way.

The vegetable and other debris in the 2·5 mm. sieve is washed thoroughly under the jet of water, and is pulled apart if necessary, although usually it is too short to be tangled. Much of it is driven through the sieve ; any that is still retained after thorough washing is added to the material accumulated in the reservoir (fig. 1, *c*) by inverting the sieve and washing out its contents. The second sieve and its guard are now washed down and removed. With the exception of the longest roots, discarded from the upper sieve, the whole sample is thus brought together in a finely divided state in the reservoir.

(3) *Removing the animals from the mineral soil.*

In the meantime, overflow water from the reservoir (fig. 1, *c*) and some of the lighter material carried by it, has been flowing over a deeply cut lip into a fourth vessel of special design (fig. 1, *f* and fig. 2). Built into this vessel is the third sieve, made of copper wire with a square mesh 0·2 mm. across. This mesh is fine enough to retain all but the smallest arthropods, but it allows the particles of clay and silt to pass into a capacious tank (fig. 1, *g*) where they settle to the bottom. For collection of very small animals that have passed through the fine copper sieve, the water overflowing from this tank can be filtered through a sieve of bolting-silk with a mesh of 0·1 mm. fastened over the end of a brass cylinder (fig. 1, *h*).

The reservoir is now tilted about its supporting pivot (fig. 1, *e*) and its contents are gradually poured into the fourth vessel. A jet of water, discharged from a long glass tube which also serves as a stirring-rod, keeps the soil in the fourth vessel in suspension and the fine sieve unobstructed. Clogging of the fine sieve is also avoided by its immersion, without air beneath it, in the settling tank (fig. 1, *g*) which is supported at such a height as to maintain the water inside and outside the vessel at a level just above that of the sieve. After a few minutes' washing, the clay and silt has all passed into the settling tank and the water jet can be turned off.

The whole sample except the long roots, the clay in the settling tank and the minute animals on the bolting-silk sieve is now in the fourth vessel. That vessel is lifted ; the water in it drains away through the copper sieve ; and the vessel is transferred to another stand. The sides of this vessel below the sieve form a funnel, the mouth of which is now closed by a rubber bung carrying a jet of compressed air (fig. 2). The air jet is turned on and then a solution of magnesium sulphate having a specific gravity of 1·2 is poured into the vessel. The air passes up through the whole surface of the sieve and bubbles through the magnesium sulphate, keeping the soil particles in suspension or at any rate not closely packed, and freeing all the organic matter that will float in a solution of such a specific gravity. After a minute or two, the bubbling is stopped by turning off the jet of compressed air ; the soil settles ; the level of the liquid is raised by adding more of the solution slowly, through a delivery tube opening under the surface ; and the floating organic material, including the arthropod animals, passes over a carefully designed lip to fall into a glass cylinder. The lower end of the cylinder is covered by a piece of bolting-silk of 0·1 mm. mesh, held in place by means of a wide elastic band. The bolting-silk sieve retains the material and allows the solution to drip into a bucket. A second period of bubbling, stirring and settling ensures that nothing having a specific gravity less than 1·2 is trapped by the soil. Any further material that rises to the surface is collected with the first. The magnesium sulphate is finally decanted from the vessel into the bucket to be concentrated and used again ; and the soil, from which all floatable material has been removed, is at last discarded.

(4) *Separating the arthropods from other organic material.*

The mass of vegetation and other organic material collected in the bolting-silk sieve is first thoroughly washed, and then put into a wide-necked flask with a small quantity of water (fig. 3, *a*). The minute animals collected from the overflow water (fig. 1, *h*) can be added at this stage but are better handled separately. About 40 cc. of benzene is poured into the flask and, with precautions against loss beside the stopper, the whole is violently shaken. Since the arthropod cuticle is wetted by benzene while most vegetable material is not, when the flask is stood at rest the arthropods accumulate on the water-benzene interface, where they can be seen lying in the benzene above the vegetable matter floating in the water beneath. In order to throw down as much vegetable matter as possible, the pressure within the flask is next reduced with a suction pump. This at first causes much of the material that has sunk in the water to rise to the interface ; but when the atmospheric pressure is restored most of the vegetation, robbed of the air which formerly made it float, now sinks.

By means of a slow jet of water, introduced below the interface, the benzene and all floating material is overflowed into a large beaker, leaving the non-floating vegetation in the flask (fig. 3, *b*). The flask is washed down and removed, and the arthropods now stand out with surprising clarity on the interface in the beaker. A binocular dissecting microscope mounted on a long movable arm is used to scan the surface, and the arthropods are easily collected with a small spoon, hammered from the head of a pin and inserted into a wooden handle. A jet of air which disturbs the benzene and makes the arthropods move over the undisturbed interface aids the eye in the final stages of collection.

This is the tedious and time-consuming part of the work. A further process has been developed which greatly accelerates the examination of soil samples for particular elements of the fauna, such as wireworms, but it was not used in any of the work described in this paper. When the entire arthropod fauna is to be investigated, no mechanism can take the place of the zoologist who has to identify, count, and separate the individuals belonging to different systematic groups. A sample of difficult clay soil can be brought to the interface stage in less than an hour and a half, but the identification and removal into vials of alcohol of a thousand or more arthropods may require three or four days.

It might be supposed that the use of metal sieves and strong jets of water would so break or crush the animals as to render their identification difficult. A few of the larger arthropods are sometimes obtained in poor condition, but the great bulk of the material is usually recovered in excellent order. Soft-bodied creatures such as pauropods and small Collembola and delicate insects such as alate aphids and fairy flies (Mymaridae) come through the process clean and complete. Moreover the parts of animals cut in two by the sampling tool, the head-capsules, legs and other chitinous fragments of arthropods already dead when the sample was taken, and cast skins, especially of aphid nymphs and beetle larvae, are also recovered by this method, which thereby provides a glimpse of the recent past as well as of the present state of the fauna.

What has been described is the method as it was developed and used where full facilities were available. In the present work, every effort was made to follow that method exactly, in order to ensure that the information collected should be comparable with the observations previously made in England. The apparatus used at Lyamungu and Kawanda was the one used in Cambridge and, as far as possible, manipulations practised in England were meticulously repeated in East Africa. Local conditions, however, imposed the following modifications. (1) Refrigeration was not available to break down the soil. Since no heavy clays were encountered no great difficulty was experienced, and an alternative, chemical, method of destroying the soil structure was not needed. (2) A bicycle pump, with a tyre valve inserted in the rubber bung of the flotation vessel, was used to bubble air through the solution. (3) For lack of a suction pump, evacuation of air from the wide-necked flask had to be omitted. (4) It is especially to be noticed that the overflow water from the settling tank (fig. 1, *g*) was not sieved through bolting-silk (fig. 1, *h*), so that any minute arthropods that had passed through the copper sieve of 0·2 mm. mesh were lost. The first three of these modifications are considered to have had no effect on the collections except in the matter of the time required to make them. The fourth modification clearly renders the collections incomplete and will be taken into account in the discussion of results.

The lack of facilities for refrigeration had another effect on the work. The disturbance of the soil during its collection exposes animals in it to their predators, and the population of a soil sample may be seriously altered if the fauna is left to interact for a lengthy period. This is one fault of the Berlese method of extracting animals from soil. Refrigeration avoids this difficulty, and the lack of facilities for it in East Africa raised the problem. Fumigation with such substances as ether is impracticable because it interferes with the benzene process, and a fumigant such as tetrachlorethane, which can be safely used for the purpose, was not available. Samples were therefore usually taken one at a time and in most cases their examination was begun within an hour of their collection. Since animals are narcotized in the magnesium sulphate and killed in the benzene, the arthropod population of these samples can be considered to have been unaltered. The few samples which could not be examined until a day or more had elapsed are indicated in the following account.

In order to make the best of the time spent at Kawanda, a number of samples taken at that centre were treated differently. Whereas all other samples were handled and examined entirely by myself, a number of duplicate samples at Kawanda were partly entrusted to W. Kanakulya, an assistant at the Agricultural Research Station. He collected the samples and carried them through the sieving and flotation processes. The organic material was then collected into bottles and, instead of being subjected immediately to the benzene treatment for the collection of the fauna, was preserved in alcohol for subsequent examination. This material was examined on my return to England without use of the benzene process, the organic matter being searched for arthropods three, and in some cases, four times.

In my judgment, these samples can be accepted as providing valid information, and they are distinguished by the letter K before their number merely in order to show which they are.

The samples were collected by means of a sampling tool which removes a cylinder of soil 4 in. in diameter and 6 in. deep. Most of those to be described in this paper comprised the soil from the surface to 6 in. depth, but on some occasions the soil from 6 in. to 12 in. deep was also examined. In the case of surface samples from pasture, the grass was clipped off at ground level with scissors and thrown away before the sample was taken ; in the case of samples from coffee and cassava plantations, any litter on the surface was first gently removed so that the animals in it should not be collected with the soil. It will be convenient to note that the area of soil surface included in a sample, 12·6 sq. in., is one part in 123·35 of a square metre.

Samples from Pasture.

Lyamungu (*Moshi District*).

The first samples examined in East Africa came from Paddock No. III at the Coffee Research Station, Lyamungu, near Moshi, Tanganyika. The paddock, lying at 4,300 ft. above sea level, was cleared of *Vernonia-Clerodendron* bush and laid down as a pasture in April 1940, after which it was used for grazing, without noteworthy cultivation, until the date of sampling. The soil is Kilimanjaro Lava Soil, " dark chocolate-brown clay loam of considerable depth, moderately friable throughout " (Stent, 1937, p. 73 ; and see his analysis p. 79). The flora of the part of the paddock sampled was principally giant star-grass, *Cynodon plectostachyum* Pilger, with a good deal of the sedge, *Kyllinga controversa* Steud., and scattered plants of *Dyschoriste radicans* Nees (Acanthaceae). The mean annual rainfall for 14 years at Lyamungu is 72·05 in. Samples were taken before and after the start of the little rains, and the following rainfall data are therefore pertinent : 1948, August, 0·44 in. ; September, 0·30 in. ; October, 2·51 in. (2·04 in. on 4th and 5th October) ; November, 1·65 in. (1·28 in. on 14th and 15th November) ; December, 6·17 in. (5·67 in. between 11th and 16th December).

Three surface samples, from 0 to 6 in., were taken from this pasture on the following dates : *Sample 4*, 9th November ; *Sample 5*, 15th November ; *Sample 24*, 27th December. Two samples from 6 to 12 in. depth were also taken from this pasture, but both were unsatisfactory. *Sample 17*, taken 16th December, was contaminated with superficial soil, which was very sticky after heavy rains and was unavoidably pushed down with the sampling tool. *Sample 25*, taken underneath *Sample 24* on 27th December, could not be examined immediately. The delay of 24 hours before its fauna was killed probably led to the loss of part of its population due to the activities of the ants, centipedes and other predators it contained. The arthropods collected from each of these samples are listed in the first five columns of Table I.

An observation of interest was made at the flotation stage during the examination of these samples. Each of the three surface samples contained a great deal of ligneous material. By " ligneous material " is here meant pieces, 1 to 5 mm. in length, of woody vegetable matter, emptied of organic contents and very buoyant in water. This material was present in a quantity very much greater than was ever observed in English pasture samples and presented new problems during the flotation and benzene processes. It was also present, but in smaller amounts, in the lower samples. This observation will be discussed below (p. 218).

Arusha Chini (*Moshi District*).

Around the southern base of Kilimanjaro is an arid steppe occupied in part by bush and in part by extensive grassy areas such as the Sanya Plains. Grazed both by game and by cattle, these grasslands are to some extent representative of very

TABLE I.

Arthropods collected from soil samples (4 ins. diameter, 6 ins. deep) from grassland in the neighbourhood of Lyamungu, Tanganyika.

	Lyamungu, 4,300 ft.					Arusha Chini 2,300 ft.		Machame North 5,500 ft.	West Kilimanjaro 6,400 ft.	
	Surface to 6 ins.			6 to 12 ins.		0 to 6 ins.		0–6 ins.	0 to 6 ins.	
Sample No.	4	5	24	17	25	20	21	22	9	10
Collembola	45	92	27	99	21	59	4	41	62	33
Thysanura	—	—	1	7	1	—	—	—	—	—
Isoptera	32	14	—	—	—	38	—	24	—	—
Psocoptera	—	2	—	—	2	3	—	—	—	—
Thysanoptera	1	5	1	—	1	10	—	—	—	3
Hemiptera	109	25	17	2	10	29	—	2	—	3
aphids	4	7	3	4	3	2	1	5	5	15
Coleoptera	—	2	—	2	—	6	2	1	23	20
larvae	3	8	3	1	3	12	4	16	10	10
Lepidoptera	2	—	3	1	—	—	—	—	10	—
Diptera	3	6	1	1	—	1	1	3	20	3
Hymenoptera	1	1	4	2	—	6	1	2	—	—
ants	6	16	8	8	4	49	1	9	8	—
Acarina	127	151	103	116	28	155	6	96	200	118
ticks	—	—	1	—	—	2	—	—	—	3
Araneida	3	—	1	3	—	2	1	2	—	—
Chernetidea	10	5	2	1	1	2	—	—	—	—
Chilopoda	—	—	1	3	3	—	—	1	5	3
Diplopoda	—	—	—	1	2	6	2	—	—	—
Palpigradi	—	—	7	—	11	—	—	—	—	—
Pauropoda	—	—	2	—	4	—	—	—	5	8
Symphyla	5	—	16	3	6	—	—	—	26	18
Total Insecta	206	178	68	127	45	215	14	103	138	87
Total Arachnida	145	156	133	127	55	167	9	99	236	150
Unclassified	14	5	6	3	4	9	2	2	15	13
Total Arthropoda	365	339	207	257	104	391	25	204	389	250

large tracts in East Africa, and for that reason alone warranted inclusion among the types of grassland to be investigated from the first centre. Furthermore, south of Moshi, at Arusha Chini, several thousand acres of such land have been brought under irrigation and now produce sugar-cane. It was therefore decided to examine soil samples from natural grassland near the sugar plantations, this area having the additional advantage for survey purposes of being at only 2,300 ft., about the lowest altitude in the region.

Samples were collected on 18th December, about one mile north of the boundary furrow of the Tanganyika Trading Company and 250 yards west of the road. Mr. F. R. Sanders, Senior Research Officer, Tanganyika Dept. of Agriculture, gave his opinion that this land had never been cultivated. It lies in a region of low rainfall. The mean annual rainfall at the Arusha Chini Estate is 16·84 ins. (11 years) ; in the three months before the samples were taken there had been a total of 1·93 ins. The tawny grey soil was volcanic ash (*cf.* Sanya soil in Stent, 1937, p. 72) to all appearances with very little humus. The dominant grasses, kindly identified by Mr. P. J. Greenway, were *Cenchrus ciliaris* (African foxtail) and *Sporobolus indicus.* Both grasses were growing in small patches of 1 to 3 sq. ft. separated by completely exposed soil, so that only about 40 per cent. of the surface was covered. The ground had clearly been burned over, as is the native custom, within a year.

Two samples were taken through grass patches and two from the bare soil beside them but, owing to shortage of time, only one of each could be examined. The arthropods collected from *Sample 20,* taken under a grass patch, numbered 391 ; those from *Sample 21,* taken from bare ground, only 25. These collections are listed in the sixth and seventh columns of Table I. Both of these samples contained a large quantity of floating ligneous material, the amount of it in *Sample 21,* from bare ground, being a matter for surprise.

Machame North (*Moshi District*).

Since Kikuyu grass (*Pennisetum clandestinum*) is an important pasture grass in the highlands of East Africa, an effort was made to examine the soil fauna under it. A pasture composed almost entirely of this species was found about two miles north of Machame Mission at an elevation of about 5,500 ft., and samples from the surface to a depth of 6 ins. were collected from it on 18th December. Machame is situated in a region of fairly high rainfall. At the mission the total for 1948 was 71·27 ins., and 4·54 ins. had fallen in 24 hours only five days before the samples were taken. No detailed description is available of the soil in the particular pasture sampled, and it must be described simply as Kilimanjaro Lava Soil, probably similar to that of a lower Machame field described by Stent (1938, p. 43 ; and see his analyses, pp. 44–45).

The examination of these samples could not be begun until 22nd December. The excessive amount of floating ligneous material then made the examination time-consuming, and in the end only one sample was finished. The arthropods collected from it, *Sample 22,* are listed in Table I. The total number is smaller than in any other surface sample from under grass. Ants were present and it is likely that they destroyed some of the fauna during the 4 days that intervened between the collection and the flotation of this sample.

West Kilimanjaro, 6,400 ft. (*Moshi District*).

The forest zone occupying the lower slopes of Kilimanjaro contains on the western side a number of rather small open glades which in some cases are occupied by a nearly pure growth of star grass, *Cynodon dactylon.* From one such glade, above Ngare Nairobi and at an altitude of 6,400 ft., two samples were taken, 10 yards apart, on 1st December. No rain gauge is situated in this uninhabited locality but, judging from the altitude and aspect, the annual rainfall is probably over 70 ins. The soil, recorded as a dark brown clay loam, and certainly a Kilimanjaro Lava Soil, contained a good deal of organic matter derived from the surrounding dense forest and the luxuriant growth of grass. Dung of elephant and rhinoceros and spoor of bushbuck were observed nearby, and it is likely that the grass is grazed by a variety of wild herbivores.

These two samples were taken by means of a light sampling tool, used for safaris on foot, which removed a cylinder of soil 6 ins. deep but only 2½ ins. diameter. The number of animals collected from them is therefore not immediately comparable with the numbers from the 4-in. samples hitherto described. For that reason, the actual numbers of animals collected from them have been multiplied by 2·56 to the nearest integer before their entry in the last two columns of Table I. *Sample 9* was done first, and the examination of *Sample 10* did not begin until 6th December. Fortunately there were no ants in this sample, but a centipede and seven small

Staphylinids may have destroyed some of the fauna during the five days' storage. Both samples contained a very large amount of ligneous material.

Kawanda (*Kampala District*).

The soil samples examined at Kawanda came from the precincts of the Agricultural Research Station, which lies at an altitude of 3,800 ft. The soil is a red earth, the B soil of the Buganda Catena (*cf.* Milne, 1936, p. 26). Since the plant ecology of the place has been described in some detail by Thomas (1945, pp. 30–35), it need only be remarked that these samples were all taken from his zone C, where the soil is an acid, reddish-brown loam overlying red clay, and where the natural vegetation would probably be elephant grass. The mean annual rainfall is 43·22 ins. (9 years) and the rain is usually distributed rather evenly throughout the year with only slight maxima centred on April and October. The rainfall in the months before and during this investigation was as follows : 1948, October 4·63 ; November 3·62 ; December 2·75 ; 1949, January 0·08 ; February 1·98 ; March 0·93. The pasture samples, all of which were taken in January 1949, were therefore collected in an unusually dry month.

Three pasture samples were taken from the grazed grass area east of the laboratory and staff houses at Kawanda. This field is occupied by a mixture of grases, including *Chloris gayana*, *Cynodon dactylon*, and *Paspalum* sp. The surface of *Sample 26*, taken on 13th January, was covered by a stool of *Chloris gayana* and a small unidentified legume. *Sample 27* was taken on 15th January from an area occupied exclusively by *Paspalum* sp. The vegetation covering *Sample K41*, taken on 18th January, was not recorded more definitely than as grass. The fourth pasture sample, *Sample K40*, was taken on 31st January from Block VII, Strip 5, one of the experimental plots at the Station. This plot had been for 2 years under *Chloris gayana* and the vegetative cover of the sample was exclusively that grass.

TABLE II.

Arthropods collected from soil samples (4 ins. diameter, 6 ins. deep) from pasture at Kawanda, Uganda.

Sample	26	27	K40	K41
Collembola	36	5	118	65
Thysanura	—	—	—	5
Isoptera	—	6	—	21
Psocoptera	3	—	1	1
Thysanoptera	4	1	—	2
Hemiptera	45	83	19	2
aphids	—	—	13	—
Coleoptera	5	—	—	12
larvae	15	6	—	1
Lepidoptera	1	1	—	2
Diptera	2	1	—	2
Hymenoptera	—	—	—	1
ants	352	389	14	14
Acarina	210	179	154	908
Araneida	—	—	—	2
Diplopoda	—	—	—	2
Symphyla	7	—	—	3
Total Insecta	463	492	165	128
Total Arachnida	217	179	154	915
Unclassified	7	—	1	—
Total Arthropoda	687	671	320	1,043
Adjusted total	349	296	320	316

During the treatment of these samples a great deal of ligneous material rose in the flotation vessel, but the amount was rather less than in the samples from the Moshi district. The fauna collected from each of these four samples is listed in Table II.

Summary of pasture samples.

From the Moshi district, eight surface samples and two from 6 to 12 ins. depth have been described. One of the surface samples, *Sample 21* from Arusha Chini, was collected from an area of bare soil, and it would be unjustifiable to include it with the other samples, all of which were collected from under grass. Disregarding that sample, the other seven surface samples set out in Table I contained an average of 306±32 arthropods. The standard error of the mean will be accepted as low, especially when the wide range of altitude, of season, and of grass cover is called to mind; and it will be agreed that these seven samples from the Moshi district are remarkably similar in the total number of arthropods collected from them.

At first sight, the four pasture samples from the Kampala district exhibit a distressing lack of uniformity. The two samples examined in Africa, *Samples 26* and *27*, were very similar, both in total population and in content. Ants completely dominated both of them, principally two very small forms, *Solenopsis* sp. and a minute ponerine. The number of ants recorded from each sample includes numerous eggs, larvae and pupae, and it is clear that both samples were taken, by misfortune, through actual ant galleries. If the ants are subtracted, the remaining arthropods in the two samples numbered 335 and 282 respectively. A collection of 320 arthropods was made from *Sample K40*. The fourth collection, *Sample K41* was remarkable for the number of mites it contained, most of them small armoured mites which in other samples were found associated with pellets of dung. W. Kanakulya made no note of observing such pellets in his sample, but he had not been asked to do so. If the number of mites in it had been the average (181) of the numbers in the other three samples, *Sample K41* would have contained 316 arthropods.

Without allowance for the fact that *Samples 26* and *27* passed through ant galleries and the suspicion that *Sample K41* contained pellets of dung, the four samples from Kawanda pasture are too diverse to provide ground for a quantitative conclusion. The mean would be 680 with a standard error of 148. If adjustments are made, if *Samples 26* and *27* are credited with only 14 ants each and *Sample K41* with only 181 mites (the average in each case of the remaining samples) the total arthropod collections would be 349, 296, 320 and 316; the four samples would be similar both in total and in content; and the mean, 320±11, would be similar to the mean of the pasture samples from the Moshi district.

In summarizing all the 11 surface samples examined from East African pastures, two courses are possible. We may take the total number of animals collected, without any adjustment, and obtain a mean population of 442±77 arthropods per sample. This mean would represent a population of 54,565 arthropods per square metre. Or we may make allowance for the obvious irregularities of three Kawanda samples and, accepting the adjusted totals mentioned above and entered at the bottom of Table II, obtain a mean population from the 11 samples of 311±20 arthropods per sample, representing an arthropod population of 38,417 per square metre in the uppermost 6 ins. of soil.

Neither of the two samples examined at Lyamungu from 6 to 12 ins. depth is satisfactory; *Sample 17* because it suffered marked contamination from the surface soil, and *Sample 25* because its examination was delayed. Since the collections made from these two samples differ widely in number, it would be unwise to draw any numerical conclusion from them. *Sample 21*, from bare ground near Arusha Chini, is of interest merely as showing the sparse population of soil long exposed to the tropical sun.

Samples from Cultivated Soil.

Under coffee.

At the request of Mr. F. R. Sanders, three soil samples were examined from his Experiment 15 (on irrigation and mulching) of which accounts will be found in the Annual Reports of the Coffee Research Station, Lyamungu. An area divided into several plots was planted to coffee in 1940. The soil in all plots was Kilimanjaro Lava Soil, similar to that of the Lyamungu pasture samples, but it was much less compacted and, at the time of sampling, was completely free of vegetation except the roots of the coffee. One sample was collected from each of three plots between 18th and 23rd November, that is, before the beginning of the rains. *Sample 6* was from plot 2-0-1, in which irrigation water is supplied so as to make up the rainfall to 4 ins. a month ; no mulch is provided ; and the coffee, grown 3 yards apart each way, belongs to clone 1. *Sample 7* came from plot 0-0-4, where no irrigation and no mulch is provided and the coffee, similarly planted, belongs to clone 4. *Sample 8* was taken from plot 0-2-1. In this plot no irrigation water is supplied but 80 lb. of banana mulch is distributed in June of each year, and the coffee is again of clone 1. These three samples were of double depth, including the soil from the surface to

TABLE III.

Arthropods collected from soil samples (4 ins. diameter, 12 ins. or 8 ins. deep) from cultivated soil at Lyamungu, Tanganyika and Kawanda, Uganda.

	At Lyamungu, Tang.			At Kawanda, Uganda					
	under Coffee			under Cassava		in fallow ground in			
						sun		shade	
Sample No.	6	7	8	34	K35	37	39	36	38
Collembola ...	61	57	46	94	7	16	35	23	19
Thysanura ...	—	—	4	—	–	—	—	—	—
Orthoptera ...	—	4	3	1	—	—	—	—	—
Isoptera	8	—	—	1	—	20	—	—	5
Psocoptera ...	—	—	—	2	—	—	—	1	1
Thysanoptera ...	—	4	4	—	—	1	—	—	—
Hemiptera ...	—	—	2	4	—	1	5	—	2
aphids ...	3	1	1	—	—	—	—	—	—
Coleoptera ...	—	2	1	—	—	—	—	1	1
larvae ...	3	2	2	16	11	46	24	16	9
Lepidoptera ...	1	1	—	5	—	—	—	—	—
Diptera	2	1	1	23	—	4	2	3	—
Hymenoptera ...	—	1	2	—	1	—	—	—	—
ants ...	5	4	3	15	3	—	—	—	—
Acarina	7	54	153	115	125	99	112	52	283
Araneida	—	—	—	3	1	—	—	1	—
Chernetidea ...	—	1	24	—	—	—	—	—	—
Chilopoda ...	—	—	3	1	1	2	—	2	1
Diplopoda... ...	—	—	2	—	—	2	—	—	—
Palpigradi... ...	—	—	1	—	—	1	6	3	4
Pauropoda ...	—	—	—	1	—	1	—	7	3
Symphyla ...	9	4	7	6	—	1	5	10	2
Total Insecta ...	83	77	69	161	22	88	66	44	37
Total Arachnida ...	16	59	190	126	127	106	123	75	293
Unclassified ...	6	7	7	0	3	0	0	1	0
Total Arthropoda	105	143	266	287	152	194	189	120	330

12 ins. deep ; and any litter present on the surface was removed before they were taken. The arthropods extracted from them are listed in the first three columns of Table III.

Under cassava.

Two samples were examined from under a crop of cassava growing in Block X, Strip 1 at the Agricultural Research Station, Kawanda. This ground had produced two crops of cotton in 1945 and 1947 with a crop of sorghum in the intervening year. In 1948 it had supported groundnuts interplanted with cassava, and the latter crop was ready for digging at the time of this investigation. *Sample 34* was taken on 28th February from a part of the plot where the fully-grown cassava provided dense shade over soil that was free of weeds but covered with a slight litter of dead leaves. This litter was removed before the sample was taken. *Sample K35* was collected on 24th January from an area where the cassava cast a less dense shade and where there was a sparse growth of weeds, particularly blue couch grass, *Digitaria scalarum.* Both of these samples were of double depth, that is, from the surface to 12 ins. deep. The animals collected from them are listed in the fourth and fifth columns of Table III.

From fallow ground.

At the request of Dr. G. ap Griffith, soil samples were examined from the site, at the Agricultural Research Station, Kawanda, of his projected experiment on the utilisation of manure. For the purposes of that experiment two adjacent areas of similar soil had been cultivated and left fallow and, at the time of sampling in late February and early March, were almost entirely free of vegetation. One area was left completely exposed to the sun ; the other was shaded by brown matting supported at a height of about 6 ft. by a light framework of poles. The two areas were to be subdivided, plots in them were to be subjected to different treatments of manure and compost, and the utilisation or loss of that manure was to be followed by means of chemical studies of the soil. Since soil arthropods are concerned in the breaking-down of manure, they constitute an important variable in such an experiment and Dr. Griffith wished to take them into account. Four samples were examined from these areas : *Samples 37* and *39* from the part exposed to the sun ; *Samples 36* and *38* from the shaded part. *Sample 38* was found, during the sieving and flotation processes, to contain pellets of rodent dung, which probably explains the large number of armoured mites found in it. Because there was not time to examine four double samples, while cultivated soil requires deeper sampling than pasture, these four samples were taken from the surface to a depth of 8 ins. The arthropods collected from them are listed in the last four columns of Table III.

Summary of samples from cultivated soil.

The nine samples from cultivated soil can be treated as a group only for very limited purposes. Living conditions in the undisturbed soil of pastures are variable enough ; in cultivated soil a large number of additional and artificial variables arise from the process of cultivation. If the samples recorded above were to be compared critically, endless enquiry would have to be made into such factors as the manner of cultivation, the time at which it was done in relation to seasonal and meteorological conditions, and the treatment to which the cultivated soil was subsequently exposed. A summary of observations based on the nine samples must be written with these limitations in mind, and the arithmetical mean of their populations should be recognised as having no numerical value except in relation to the fact that the samples were from cultivated soil.

The average number of arthropods in the nine samples is 198±26, representing a population of 24,423 arthropods per square metre. This is significantly lower than the adjusted mean (311 ± 20) of the pasture samples, and the difference is greater than appears from simple comparison of these two figures because the pasture samples were only 6 ins. deep while four of these were 8 ins. and five were 12 ins. deep. The only quantitative conclusion that can safely be drawn is that the arthropod population of these cultivated soils was much less than that of adjacent pasture land.

Discussion.

Quantitative information about the arthropod fauna of tropical soil is extremely scanty. A good deal of the work that has been cited as a source has to do with the animals frequenting litter on the surface rather than those inhabiting the soil itself. This is true of the collection made by Beebe (1916) from Brazilian forest debris ; of the list published by Wolcott (1924) of the animals found on 3 sq. ft. of pasture in Puerto Rico ; of two papers by Dammerman (1925, 1937) on the " soil and surface fauna " in the Dutch East Indies ; and of an admirable account by Williams (1941) of the fauna of the ground stratum in the rain forest of Panama.

Only two workers appear to have published quantitative information about the arthropods inhabiting the soil in tropical countries. Van Zwaluwenburg has written two papers (1926, 1931) about the soil fauna of sugar-cane fields in Hawaii. He sampled fallow ground, which had been under sugar-cane and in which there was still much root material, almost weekly from May 1925 until July 1926, taking a total of 51 samples. He also sampled ground on which there was growing sugar-cane nearly every fortnight from March 1925 until August 1926, with a total of 35 samples. The samples taken were 1 sq. ft. on the surface and 9 ins. deep. The method used to extract the animals from the soil is not mentioned. The average number per sq. ft. of surface is given approximately for some items of the fauna, but the main results are expressed as percentages of the average total populations, and the latter are recorded only to the nearest million per acre. The average population of the fallow ground is given as 57 million animals per acre (which is 14,085 per square metre), and that of the soil under sugar-cane as 72 millions per acre (which is 17,792 per square metre). These high numbers, and the small size of some of the animals collected, suggest that the examination of the samples was thorough, and it is a pity that the results of all this labour have not been published in more detail.

Using a modification of our method, which had been demonstrated to him in Cambridge, Strickland (1945) studied a number of soil samples from three forest reserves and four cacao estates in Trinidad. Each of his samples consisted of five cores, 3·6 ins. in diameter, put together and examined in bulk. The surface area of such a composite sample would be 50·9 sq. ins. By adding the appropriate columns of his Table 2, it can be calculated that in the litter and leaf mould on the surface, of which 13 samples were taken, an average population of 11,893 arthropods per sq. metre was found ; and in the soil from the surface to 9 ins. in depth, of which seven samples were taken, a population of 13,783 arthropods per square metre. The latter number is similar to that found by van Zwaluwenburg in the same depth of soil ; and these two may be compared with the population of 23,511 arthropods per sq. metre found in the uppermost 12 ins. of soil, without litter, in the five samples described above from coffee and cassava plots.

A second paper by Strickland (1947) describes the examination of additional samples of the same surface area but only 3 ins. deep. In this second investigation the fauna was extracted by means of Berlese-Tullgren funnels. Six composite samples from a cacao plot provided collections which represent a population of 25,004 arthropods per sq. metre in the surface litter and 11,065 in the soil from the surface to 3 ins. deep. Six composite samples from a plot of grass that had been mown at fortnightly intervals yielded 2,693 arthropods in the uppermost 3 ins. of soil ; and six more from a sub-plot left unmown during the sampling period of 3 months yielded 4,962, which numbers represent 13,669 and 25,187 arthropods per sq. metre respectively.

These last samples from grassland are of particular interest from the point of view of the present paper, as affording a partial comparison between pasture samples in Trinidad and in East Africa. Strickland did not take any of his grassland samples deeper than 3 ins., but in his samples from forest reserves and cacao estates, the population he found between 3 and 6 ins. depth was 33·65 per cent. of that between the surface and 3 ins. If the same proportion had occurred in his grassland site, the population under grass in Trinidad would have been 18,269 arthropods per sq. metre under the mown grass and 33,662 under the long grass. The latter number is in the same order as the population (38,417) found under pasture in East Africa.

It is the special value of the collections described in the present paper that they were made by the same method, with the identical apparatus, and even with the same idiosyncrasies of manipulation, as collections already recorded from English pastures. They therefore allow for the first time a quantitative comparison to be made between the arthropod faunas of tropical and temperate soil.

On the side of the tropical soil, the samples worth comparing are those from pasture summarised above on page 212. Eleven samples from several different pastures and representing a wide range of environmental conditions gave a mean collection of 442±77 arthropods per sample, representing a population of 54,565 per sq. metre ; or, if three collections are adjusted in conformity with biological observations, of 311±20 arthropods per sample, or 38,417 per sq. metre in the uppermost 6 ins. of soil.

On the side of the temperate soil, care must be taken that the numbers used are properly comparable. Twenty samples collected in England in November (Salt & others, 1948, Tables 1 and 2) had an average of 2,137 arthropods per sample, representing a population of 263,658 per sq. metre ; but for two reasons this number cannot be used for comparison with the African samples. In the first place, the 20 English samples included the soil from the surface to a depth of 12 ins. while the African samples were only 6 ins. deep. In the second place, some of the English samples were examined with the aid of an extra component not used in Africa. That component, which filtered the overflow water, was found in England to recover a large number of minute animals, especially small mites, which were lost when it was not used.

Fortunately there are available for comparison 25 pasture samples examined in England without the use of the extra component. Twenty of them, studied in May 1943 and recorded in Table 3 of the paper cited above, gave a collection of 18,150 arthropods, of which 12,399 were in the upper cores, from the surface to 6 ins. deep, and 5,751 in the lower cores, from 6 ins. to 12 ins. deep. The first five samples collected from the same pasture in November 1943 and set out in Table 1 of the same paper, were also examined without the extra component. They contained a total of 7,793 arthropods, 5,890 in the upper and 1,903 in the lower cores. The upper parts of these 25 samples can be regarded as completely comparable for our present purposes with the East African pasture samples. Because they have never been separately recorded and in order to allow comparison, these 25 upper samples are set out in Table IV. The total number of arthropods collected from them was 18,289 and they contained on the average 732±64 arthropods per sample, representing a population of 90,238 per sq. metre.

From a comparison of these two lots of samples, it appears that the arthropod population in the uppermost 6 ins. of East African pasture soil is only about half as large as that in an English pasture. This conclusion is borne out by all observations

TABLE IV.

Arthropods collected from 25 soil samples (4 ins. diameter, 6 ins. deep) from Spinney Pasture, Cambridge, in May and November 1943.

Station	Collembola	Thysanura	Psocoptera	Thysanoptera	Hemiptera	Coleoptera	Lepidoptera	Diptera	Hymenoptera	Acarina	Araneida	Chernetidea	Chilopoda	Diplopoda	Symphyla	Total Insecta	Total Arachnida	*Unclassified	Total
May																			
1	95	*	*	1	2	15	—	4	—	216	—	—	—	—	*	117	216	11	344
2	310	*	*	1	3	19	—	3	—	232	3	—	1	—	*	336	236	8	580
3	185	*	*	—	6	15	—	—	1	204	—	—	—	1	*	207	205	5	417
4	325	12	—	3	6	18	1	45	—	532	—	—	1	2	—	410	535	—	945
5	190	3	—	2	19	45	—	2	5	488	1	—	2	—	3	266	494	—	760
6	222	9	1	—	39	46	1	5	—	468	—	—	3	—	3	323	474	—	797
7	310	5	—	2	1	19	1	1	—	415	—	—	2	1	14	339	432	—	771
8	112	3	—	3	9	10	—	3	1	350	—	—	1	—	11	141	362	—	503
9	219	16	—	1	16	24	1	—	2	274	3	—	1	—	6	279	284	—	563
10	96	8	—	7	32	18	1	6	1	432	—	—	—	—	—	169	432	—	601
11	23	4	1	2	11	30	1	2	11	316	3	—	—	3	10	85	332	—	417
12	228	22	1	2	2	19	—	2	1	343	4	—	3	2	18	277	370	—	647
13	61	2	1	1	5	12	—	2	—	236	—	—	2	—	6	84	244	5	333
14	174	14	—	34	7	20	1	8	1	666	6	—	5	2	6	259	685	—	944
15	92	5	—	8	13	17	—	4	—	418	—	—	1	3	24	139	446	—	585
16	138	28	2	9	25	30	—	5	1	399	4	—	3	5	16	238	427	—	665
17	105	18	—	2	15	33	2	1	1	310	—	—	2	2	3	177	317	—	494
18	91	8	1	12	32	20	—	1	1	398	2	—	3	1	4	166	408	6	580
19	88	25	1	20	13	18	1	7	—	529	1	—	4	5	9	173	548	—	721
20	174	32	—	26	24	31	—	3	3	431	1	—	—	3	3	293	439	—	732
Nov.																			
1	340	—	—	3	40	8	—	3	—	239	—	—	—	—	—	394	239	—	633
2	1,036	—	—	13	14	8	—	3	—	610	—	—	3	—	—	1,074	613	—	1,687
3	172	144	—	2	59	28	1	4	—	608	—	—	2	1	5	410	616	—	1,026
4	283	77	—	7	83	16	—	2	1	811	—	1	1	—	1	469	814	—	1,283
5	105	2	—	2	48	30	1	8	3	1,054	5	—	2	1	—	199	1,062	—	1,261
Total	5,174	427	8	163	534	549	12	124	33	10,979	33	1	43	32	142	7,024	11,230	35	18,289

* These Thysanura, Psocoptera and Symphyla were not separately recorded at the time of collection and cannot now be classified.

made and impressions received while the work in Africa was in progress. It could be invalidated, so far as the samples examined are concerned, only if there had been present in the tropical soil a much larger proportion than in the English soil of the minute arthropods that can be washed through a sieve of 0·2 mesh. A thorough study on a larger scale than was possible in this single-handed and exploratory survey may alter the view but, so far as the available information goes, the arthropod population of tropical pasture soil must be accepted as much smaller than, and only about half as large as, that of temperate grassland.

The causes of this smaller arthropod population in tropical soil are doubtless complex and call for special investigation, but one among them is outstanding, that is the high temperatures to which the surface soil is exposed. In English pastures the bulk of the arthropod fauna occupies the upper layers of soil. This aggregation of the fauna in the upper layers is partly due to such factors as the better aeration and greater amount of food near the surface, but it is perhaps principally due to the larger size of the pore spaces in the upper soil, for these provide the living space for the most numerous groups, the Collembola and mites. Under tropical conditions, however, the uppermost layers of soil are strongly heated by the sun and are sometimes uninhabitable. A small part of the fauna may be able to make daily movements up and down in the soil, but the great majority of the arthropods are too small and weak to move far. These, therefore, are forced to live in a restricted range, limited above by diurnal heat and below by lack of food and air and of spaces to live in.

The consequences of the smaller arthropod population are as involved and as much in need of investigation as its causes. From a zoological point of view, an immediate question arises as to the influence of the meagre population on the balance of life in the soil. The arthropods have direct interactions with the larger fungi and with nematode and enchytraeid worms, and probably have indirect effects on the smaller fungi, protozoa and bacteria. If the arthropod population is different, the status of these groups is likely also to be different in temperate and tropical soils. Information does not yet exist for a fruitful discussion of that matter in quantitative terms. But it is necessary to discuss briefly what appears to be, at least partly, another consequence of the small arthropod population, that is, the abundance of ligneous material repeatedly observed in samples of East African soil.

Throughout the examination of the pasture soil described above, the amount of ligneous material that came up in the flotation vessel was remarkable (see pages 208 and 210 above). The material concerned was composed of pieces of vegetable matter retaining their form and recognizable as bits of stalk or twig, but completely emptied of soft parts and apparently composed exclusively of the woody skeleton. Most of these pieces were between 1 and 5 mm., long but some were larger. They were all very buoyant in water and the pale grey of weathered wood in colour, both of these properties being partly due to the air enclosed within their cavities. The impression given by visual examination of this material was that of vegetable debris emptied of its cellular contents by decomposition but never finely comminuted.

This ligneous material was clearly vegetable debris that had escaped mastication by the mouthparts of herbivorous arthropods and trituration in the gizzards of earthworms. That larger quantities of vegetable matter should escape those comminuting processes in the African soil examined than in English soil may be attributed to two factors. (1) The arthropods have been shown above to have been present in much smaller numbers than in English soil. Earthworms are known to be relatively scarce in many tropical soils and were notably few in the samples examined. There were therefore fewer animals present than there would be in a temperate pasture capable of breaking down small pieces of vegetation. (2) Decomposition of vegetable debris by bacterial and fungal activity is accelerated by heat and proceeds rapidly at the high temperature of the surface soil in East Africa. The period during which fallen vegetable matter remains attractive and palatable to arthropods and earthworms is therefore shortened.

Both of these factors so operate as to increase the amount of decomposed but uncomminuted ligneous material that is formed. Further, once it has been formed that material tends to persist by reason of its unattractiveness to the arthropods, and the scarcity of earthworms that might ingest it indiscriminately with the soil.

This line of thought can be taken a step further. A leading textbook on soil (Russell, 1950, pp. 244–245) states, " . . . humus appears to be built out of two groups of material—oxidised lignin and by-products of the metabolism of the soil organisms. The outstanding feature of humus formation in soils appears to be the importance of the alimentary canals of the soil fauna." Many tropical soils are poor in humus and fail to maintain their humus content under cultivation. Is it not likely that the abundance of ligneous material in my samples and the humus deficiency of tropical soils are alike due to the absence of a sufficient population of soil animals capable of comminuting the plant debris and, by passing it through their alimentary canals, bringing about the conversion of lignin to humus? These considerations suggest, at least, that some of the problems of humus formation in the tropics need re-examination with particular reference to the status of the arthropod and oligochaete populations of the soil.

Summary.

A method is described for the extraction of arthropods from soil.

Eleven soil samples from pastures in the neighbourhood of Moshi, Tanganyika, and at Kawanda, Uganda, yielded collections representing a population of 54,565 arthropods per sq. metre in the top 6 ins. of soil or, if three samples are adjusted in conformity with biological indications, of 38,417 per sq. metre.

Nine soil samples from coffee and cassava plantations and from fallow ground gave collections representing a population of 24,423 arthropods per sq. metre in the top 12 ins. (in some cases 8 ins.) of soil.

Twenty-five soil samples from a pasture near Cambridge, examined in a strictly comparable manner, gave collections representing a population of 90,238 arthropods per sq. metre in the top 6 ins. of soil.

It appears that the arthropod population in the uppermost 6 ins. of East African pasture soil is much smaller than, and only about half as large as, that in an English pasture.

The causes and consequences of the smaller arthropod population of tropical soil are briefly discussed, and a connection is suggested between the meagre arthropod (and earthworm) population and the large amount of ligneous material found in the soil samples examined, This connection may also bear on the paucity of humus in some tropical soils.

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THE EFFECT OF A DIFFERENCE IN TEMPERATURE AND HUMIDITY ON CERTAIN REACTIONS OF FEMALE *AËDES AEGYPTI* (L.).

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In his report on the 1943–45 Cambridge Mosquito Repellent Enquiry, Sir Rickard Christophers (1947) described some experiments in which the attractiveness of certain stimuli associated with the human body surface for *Aëdes aegypti* (L.) adults was tested. His results showed certain marked differences from those of some similar experiments independently performed by the writer (1948), and the purpose of the experiments described here was to test the hypothesis that these differences were due to a difference in the ambient temperature and humidity.

In both investigations, mosquitos were confined in a glass tube, large enough to allow them to fly freely inside, closed at either end by mosquito netting. The response to different stimuli was tested by applying them to one end of the tube, the mosquitos being in most experiments unable actually to touch the test object, either with their tarsi or their probosces. Christophers assessed the magnitude of the response by comparing the total number of individuals in the half-of-the-tube nearest the stimulus with the total number in the other half. The writer assessed it (*a*) by comparing the number of individuals counted on the netting near the test stimulus at given intervals with similar counts made when no test stimulus was present, (*b*) by similar comparative counts of the numbers alighting on or leaving the netting, this being to measure the degree of activation induced, and (*c*) by counting the numbers probing.

With his technique, Christophers found that *A. aegypti* females exhibited a definite positive response to a warm dry surface at a temperature of 40°C. This was enhanced if the surface was moistened, but only slightly. With moisture at room temperature no positive reaction was observed. The writer, on the other hand, found that while a warm moist surface induced almost, or perhaps quite, as great a response as the intact palm of the human hand, a dry surface at temperatures varying from 36°C. to 40°C. had no discernible effect. A moist surface at room temperature, again in contrast to Christophers' results, induced a quite definite positive reaction as measured by all three criteria.

The difference between Christophers' method of assessing the response and the writer's could clearly not account for these sharply defined differences. Differences in the general viability of the females also seemed unlikely to be responsible, for the response was greater in one case, less in the other. The most probable explanation seemed to lie in the fact that whereas Christophers' experiments were carried out at an ambient temperature of 25°C. and a relative humidity of 80–90 per cent., the writer's were done at 28°C. and a relative humidity of 50–70 per cent. This hypothesis, if correct, appeared to carry implications beyond the scope of the immediate problem ; it suggested that behaviour reactions of the type under consideration were more dependent on the precise climatic conditions to which the insect was subjected than was generally realised.

The relevant experiments were therefore repeated under the temperature and humidity conditions employed by Christophers, and under those previously employed by the writer. Except in regard to temperature and humidity, conditions in the two sets of experiments were now identical ; previous small differences in technique, or possible physiological differences between the strains of mosquitos employed, were therefore eliminated.

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The word " attraction ", as before, will be used to describe the process by which an individual is induced to fly towards, and alight as near as possible to, the source of stimulation ; it will not be used in connection with probing.

Material and Methods.

The rearing and experimental room, except when different conditions were required, was maintained at 25°C. and 60–80 per cent. R.H., the humidity being kept at the desired level by regulation of a fan directing a current of air over an exposed surface of water. When a very high humidity was needed, the water was heated. The required temperature was maintained by thermostatically-controlled electric heaters.

The apparatus was essentially as before. It consisted of a horizontal glass tube, 27·5 cm. in length, 5 cm. in diameter, fitting at either end into a hole in a thick cardboard screen. A cardboard ring, over the inner face of which a piece of mosquito netting was stretched, was inserted into each end of the tube. The thickness of the ring was 1·5 cm., so that when a test surface was applied to one end of the tube, mosquitos confined inside it were separated from the test surface by precisely this distance. The whole apparatus was placed inside a chamber lined with white paper, in one side of which were apertures allowing for observation and manipulation. Illumination was diffuse and overhead.

The stimuli tested were a warm dry surface, a moist surface at room temperature, and, occasionally, as a check on the reactivity of the insects, the palm of the experimenter's hand. To obtain a suitable warm surface the rather clumsy arrangement formerly employed was abandoned in favour of one similar to that adopted by Christophers. It now consisted of one face of a small straight-sided copper box containing water, the temperature of which was raised to the required level by a small electric bulb fitted inside. Two thermometers fitting into the box at different levels gave the temperature of the water, which was without any difficulty kept constant to within 0·5°C. by hand operation of a switch connected to the electric bulb. It was assumed that the temperature of the outer surface of the box did not differ significantly from that of the water inside. Since the warm surface employed by Christophers was at 40°C., while in most of the writer's previous experiments it was at 36°C., the response to both temperatures was retested. The moist surface at room temperature (the " cold moist surface ") was, as before, a small water-saturated filter paper of standard size allowed to adhere by its own surface tension to a vertical glass surface.

As before, females to be used in experiments were allowed to feed only on sugar solution. This was available up to the time of the experiment, but no female whose abdomen was swollen with fluid was used ; preliminary experiments indicated that such females were more responsive than those deprived of sugar solution since the day before. Light anaesthesia was necessary so that suitable females could be selected, and for this purpose ether was once again employed ; carbon dioxide was tried as an alternative but since females so treated were no more responsive than those which had been etherised this was not continued. An hour was allowed for recovery from the effects of the anaesthetic ; all females seemed as active after this period as before anaesthetisation, and few showed any signs of sluggishness after only half as long. The age of the females was always between two and ten days from emergence. Adherence to the lower age limit seemed desirable as various authors (Macfie, 1915 ; Gutzevich, 1931 ; Seaton & Lumsden, 1941) found *A. aegypti* females reluctant to bite at an earlier age. The upper age limit was probably rather less important, as in the writer's previous experiments females 20–30 days after emergence gave no evidence of being less responsive to the stimuli presented than younger females.

As mentioned earlier, in the previous work counts were made, both of the numbers on the netting at given intervals, and of the numbers alighting or leaving over a given period. The latter was found to be essential for a true comparison of the attractiveness of different stimuli. Thus, with some stimuli, females once having alighted on the netting rarely moved away. With other, and more activating stimuli, a female having alighted usually proceeded to move to and fro, so disturbing others. Both disturbed and disturbing females then usually flew away, shortly, as a rule, to re-alight. The effect of activation was thus that at any given instant a considerable proportion of the females which would otherwise have been on the netting were elsewhere in the tube. Counts of the numbers alighting or leaving gave some measure of the magnitude of this effect, and were previously considered in conjunction with the numbers *on* the netting in comparing the attraction exerted by different stimuli. In the present investigation the numbers alighting have similarly been considered in comparing the attractiveness of one given stimulus under different conditions.

As both the numbers on, and alighting on, the netting were to be taken into consideration in assessing the response to a given stimulus at a given time, it was clearly desirable that they should be counted simultaneously. This was formerly impracticable, but in the experiments described here the activating effects of the stimuli tested were small enough for it to be feasible. To facilitate it, the number of females in the tube was reduced from 30 to 15.

The probing reaction, though not necessarily induced by the same stimuli as those inducing the mosquito to fly towards, and alight as near as possible to, a source of stimulation, provides another means of measuring the response to a given stimulus. As before, the number of females on the netting probing at each time of counting were noted, and the proportion probing calculated.

The experimental procedure was thus as follows. The temperature and humidity of the room were adjusted to the required level, and the number of females on the netting at one end of the tube counted at ½-minute intervals over a 5-minute period. Note was taken of how many of the females were probing, and of the total number alighting on the netting during the 5-minute period. A test surface was then applied to the same end of the tube, and, after an interval of 1 minute to allow its emanations to diffuse in, exactly the same observations over the same period as before were made. The test surface was now removed, and after a 10-minute interval the process was repeated at the opposite end of the tube with a different type of test surface. Two or three sources of stimulation were tested in this way. The tube was then turned through 180°, and the whole series of observations repeated.

At first the response to a series of stimuli under the two temperature and humidity combinations was observed on the same day with the same insects. This did not prove wholly satisfactory as the required alteration in conditions usually took over an hour to effect, and the females tended to be less reactive during the later part of the experiment. In subsequent experiments, different conditions were obtained on consecutive days, fresh females from the same cage being used each day. The order in which the two temperature and humidity combinations were employed was reversed in each successive pair of experiments, and the order in which the different types of stimulus were applied was varied regularly from experiment to experiment.

To reproduce the conditions of Christophers' experiments a temperature of $25\pm0{\cdot}5$°C. and a relative humidity of 85–90 per cent. was obtained. In repeating the conditions of the writer's earlier experiments it seemed desirable to obtain a less variable humidity than the previous 50–70 per cent. R. H.; since it had, in fact, been usually nearer the lower figure, 50–55 per cent. R.H. was chosen. The temperature was $28\pm0{\cdot}5$°C.

In presenting results, the number of females counted on the netting near a source of stimulation (test count), and the number counted during the previous control period (control count), were formerly combined into an " Index of Attraction ". This was the test count expressed as a percentage of the test plus the control count. It was a convenient measure but one which appeared on further reflection to have no advantages over the simpler procedure of subtracting the control from the test count ; if anything, this is a more reliable measure of the response. This method of assessment has therefore been adopted, d_o being the difference between the test and control counts of the number of females *on* the netting, d_a the difference between the test and control counts of the numbers *alighting* on the netting. The number probing during exposure to a source of stimulation is expressed as a percentage (p) of the total number counted on the netting during that exposure. A female very

TABLE I.

The response to warm dry and cold moist surfaces.

Source of stimulation	No. of expt.	Age of females (days)	28°C., 50–55% R.H.					25°C., 85–90% R.H.				
			o	d_o	a	d_a	p	o	d_o	a	d_a	p
Warm dry surface (36°C.)	1	3–9	64	−22	17	+14	43·8	45	+ 4	23	+23	77·8
	2	4–10	43	− 5	12	+11	20·9	68	− 2	33	+33	41·2
	3	4–7	136	+31	16	+15	0·7	114	+55	38	+26	11·4
	4	2–9	104	− 2	4	+ 3	4·8	89	+11	31	+30	30·3
	5	2–7	98	− 1	5	+ 4	2·0	79	+14	25	+21	41·8
	6	3–7	113	+ 7	2	+ 1	1·8	129	+60	52	+49	50·4
	7	2–8	31	− 9	1	0	6·5	71	+24	19	+14	26·8
	8	2–8	117	+13	18	+16	12·0	110	+21	1	− 4	11·8
Means				+ 2		+ 8	12		+23		+24	36
Warm dry surface (40°C.)	1	3–9	98	+20	82	+77	70·4	90	+33	49	+47	67·8
	2	4–10	51	+ 6	15	+13	72·5	37	+ 7	19	+19	62·2
	3	4–7	102	+30	4	0	7·8	117	+22	46	+37	17·1
	4	2–9	81	+20	3	+ 2	2·5	109	+33	35	+35	48·6
	5	2–7	116	+36	4	+ 4	4·3	97	+14	14	+ 8	40·2
	6	3–7	96	+ 3	15	+13	30·2	119	+15	56	+46	64·7
	7	2–8	62	− 8	7	+ 7	19·4	70	+ 2	14	+10	34·3
	8	2–8	94	+19	17	+16	12·8	98	− 2	14	+14	55·1
Means				+16		+17	28		+16		+27	49
Cold moist surface (room temperature)	1	3–9	113	+22	58	+54	38·1	47	+ 7	1	− 3	4·3
	2	4–10	73	+24	26	+22	32·9	58	+ 3	20	+19	36·2
	3	4–7	132	+41	23	+19	9·8	73	+19	9	+ 3	0·0
	4	2–9	92	+32	19	+19	12·0	111	+ 4	5	− 1	0·0
	5	2–7	70	+20	3	+ 3	4·3	74	−12	2	0	1·4
	6	3–7	138	+30	27	+22	5·8	113	+19	3	− 4	0·0
	7	2–8	126	+34	18	+14	17·5	106	+ 2	1	0	0·9
	8	2–8	125	+25	28	+24	19·2	110	+ 8	0	0	0·0
Means				+29		+22	18		+ 6		+ 2	6

o = Number of females counted *on* the netting near the test surface at half-minute intervals over 5-minute period.

d_o = o minus the corresponding control count.

a = Number of females *alighting* on the netting near the test surface over 5-minute period.

d_a = a minus the corresponding control count.

p = percentage probing.

occasionally probed for a short time during the control period ; in such cases the control count (probing) has been deducted from the test count before estimation of the final percentage.

Results.

The results of testing the response to a warm dry surface (36°C. and 40°C.) and to a cold moist surface at an ambient temperature and humidity of 28°C./50-55 per cent. R.H. and 25°C./85–90 per cent. R.H. are shown in Table I. In the first two experiments both sets of observations were made on the same day ; in the rest, on consecutive days. It should be borne in mind that the fact that a stimulus produces a significantly higher value for d_o under one set of conditions than another does not indicate a greater degree of attraction unless d_a is also higher, or at least equal, under the same conditions. If it is not, a high value for d may be simply a consequence of a low degree of activation.

The means shown in the Table suggest at once that there was a tendency for the response to the warm surfaces to be greater at 25°C./85–90 per cent. R.H. than at 28°C./50–55 per cent. R.H., and that the reverse was true of the response to the cold moist surface. But with such a high degree of individual variation, means may mislead ; a more valid comparison can be made if the results of each pair of experiments are compared individually. The accompanying histogram (fig. 1) has been constructed so that this can be done at a glance. The numerals on the left-hand border are the serial numbers of the experiments. From top to bottom, it is divided into three sections, each dealing with a different source of stimulation. From side to side it is divided into two, the left-hand section dealing with attraction, the right-hand with probing. Both right- and left-hand sections are divided by a mid-vertical line, each side of which represents one of the temperature and humidity combinations. A difference in the degree of attraction exerted by a given stimulus under different conditions has been plotted by drawing (*a*) an area proportional to the difference between the two values of d_o obtained, and (*b*) an area proportional to the difference between the values of d_a, the area being drawn on the side representing the conditions which produced the higher figure. Areas of type (*a*) are shown only in outline, those of type (*b*) are blocked in. Differences in the proportions probing have been plotted in exactly the same way, the areas being again blocked in. An area drawn one side of one of the mid-vertical lines thus indicates a higher response under the conditions represented by that side than under the conditions represented by the other side, the extent to which this is so being indicated by the size of the area.

It will be seen that with the warm surface at 36°C. both d_o and d_a were greater at 25°C./85–90 per cent. R.H. than at 28°C./50–55 per cent. R.H. in seven of the eight experiments. It can therefore be stated that in these seven experiments a greater degree of attraction was exerted under the former than under the latter conditions, though it must be admitted that in only one experiment (No. 6) was the difference really pronounced. In the remaining experiment the result was inconclusive, d_o being greater under the one set of conditions, d_a greater under the other. With the warm surface at 40°C., both d_o and d_a were greater at 25°C./85–90 per cent. R.H. in only four experiments, in two of which the differences were very small. In one experiment, both d_o and d_a were greater at 28°C./50–55 per cent. R.H., while in the remaining three, d_o was greater under one set of conditions, d_a greater under the other. Thus in four out of eight experiments the attraction exerted was greater at 25°C./85–90 per cent. R.H., though never very conspicuously so, in one it was greater at 28°C./50–55 per cent. R.H., and in three the results were inconclusive. With the cold moist surface both d_o and d_a can be seen always to have been greater at 28°C./50–55 per cent. R.H. than at 25°C./85–90 per cent. R.H., the differences

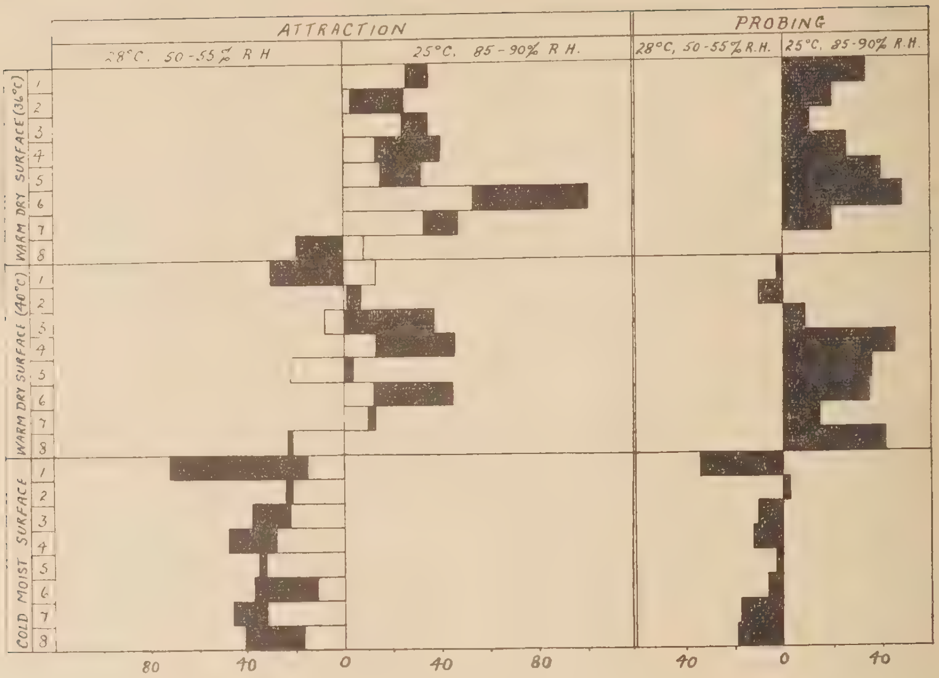

Fig. 1.—The effect of a difference in temperature and humidity on certain reactions of female *Aëdes aegypti* (L.).

being moderately well defined. It can thus be said that this source of stimulation was consistently slightly more attractive under the former conditions.

Probing in response to the warm surface at 36°C. was greater at 25°C. /85–90 per cent. R.H. than at 28°C. /50–55 per cent. R.H. in all except one pair of experiments, in which it was equal, though the magnitude of the difference varied considerably. With the warm surface at 40°C. the response was greater at 25°C. /85–90 per cent. R.H. in six experiments, the difference being well-defined in four of these. In the remaining two experiments the response was greater at 28°C. /50–55 per cent. R.H., the differences being slight. With the cold moist surface *p* was greater at 28°C. / 50–55 per cent. R.H. in seven experiments, in only one of which was the difference pronounced. In the remaining experiment *p* was very slightly higher at 25°C. /85–90 per cent. R.H.

In view of the degree of variation between the results of the comparatively small number of experiments performed, caution must be exercised in drawing conclusions. It does seem, however, that under the conditions of the experiments a warm dry surface at 36°C. is more attractive and more evocative of probing at 25°C. /85–90 per cent. R.H. than at 28°C. /50–55 per cent. R.H. In lesser degree, the same appears to be true of the response to a warm surface at 40°C. A moist surface at room temperature, on the other hand, appears to be less attractive and to produce less probing at 25°C. /85–90 per cent. R.H. than at 28°C. /50–55 per cent. R.H.

Conclusions.

The question now arises as to whether the differences in response observed in the above experiments are a sufficient explanation of the difference between the results obtained by Christophers, and those obtained in the writer's earlier experiments. Apparently they are not, for in the experiments described here the warm dry surface frequently exerted some degree of attraction and always induced probing at 28°C. / 50–55 per cent. R.H. (see Table I), while in the writer's previous experiments under the same conditions there was no definite evidence of attraction and probing was never observed. With the cold moist surface, the converse appears to be true. In the 12 experiments performed previously, the mean value for d_o with cold moisture was $+62$. In four experiments in which appropriate observations were made the mean value for a (d_a was not estimated) was 43, and the mean proportion probing 22 per cent. Corresponding figures for the eight experiments described here are $+29$ (d_o), 25 (a) and 18 per cent. (p). In so far as means are to be relied upon, the indication is thus that there was a tendency for the cold moist surface to be more attractive in the former experiments. The difference between the proportions probing cannot be considered significant.

The results of experiments performed at 25°C. /85–90 per cent. R.H., the temperature and humidity employed by Christophers, can not readily be compared with the results obtained by Christophers himself as his method of measuring the response was different. He was concerned only with attraction and does not quote the numbers probing. So far as the results are comparable, there is no evident discrepancy between them. In both cases a warm dry surface at 40°C. was observed to exert a definite positive attraction, and while Christophers obtained no evidence of attraction with a cold moist surface, whereas in the writer's present experiments a slight one was sometimes apparent, this was not sufficiently consistently displayed to indicate a definite discrepancy.

It is unlikely that any difference in the general viability of the females can account for the difference between the results presented here and those previously obtained by the writer, for the response was higher with one type of stimulus and lower with another. The females were frequently of the same age groups, so an age effect is also improbable. The most likely explanation seems to lie in a conditioning effect of the temperature and humidity conditions under which the insects were reared. In the writer's previous experiments the temperature of the rearing and experimental room was 28°C. and the relative humidity 50 to 70 per cent., usually between 50 and 60 per cent. In the experiments described here the rearing and experimental room—except during actual experiments, which occupied only a small fraction of the total time—was at 25°C. and a relative humidity of 60 to 80 per cent., usually between 65 and 75 per cent. The temperature at which the insects were reared was thus lower, and the humidity on the average higher, than formerly. This may well account for the higher response to a warm dry surface, and apparently lower response to a cold moist surface, observed in the present experiments.

This suggestion implies that a temperature and humidity difference operating before the experiment can so condition the females as to produce the same type of difference in response as can a similar temperature and humidity difference operating during the experiment. This, if true, offers a likely explanation of the whole of the difference between the results obtained by Christophers and those formerly obtained by the writer ; in both investigations the insects were exposed to the temperatures and humidities at which the experiments were performed from, or very nearly from, the time of emergence. Had the present experiments been so arranged that the insects were subjected to different conditions prior to, as well as during the experiments, a very much more clearly-defined difference in response would perhaps have been observed.

It is interesting that in a recent preliminary note, Brown (1951) describes some field experiments with various species of *Aëdes* (not including *aegypti*) which bear out strikingly the supposed conditioning effect of temperature and humidity on behaviour. Speaking of warmed steel tanks covered with clothing, Brown states that " at air temperatures above 60°F., a robot with moistened clothing attracted two to four times as many mosquitoes as one with dry clothing. At cooler temperatures, and particularly at high humidities, the results were the reverse ; the dry clothing attracted up to twice as many mosquitoes as the moist, despite the fact that the temperature of the surface of the dry clothing proved to be 1–3°F. lower than that of the moist ". It will be remembered that while the writer found the moistening of a warm surface greatly to increase its attractiveness, Christophers, working at a lower temperature and higher humidity, found a warm surface to be only slightly more attractive when moist than when dry. Though the differences he observed are very much more extreme, Brown's results, so far as they are comparable, are thus consistent with the differences described here.

It may be concluded that the response of female *A. aegypti* to a warm dry surface and to a moist surface at room temperature is conditioned by the temperature and humidity to which they are exposed at the time of the experiment, and probably also by those to which they have been exposed prior to the experiment. This certainly accounts for part, and quite possibly all, of the difference between the attraction observed to be exerted by these two stimuli by Christophers, and that observed in the writer's earlier experiments. If it is true that a difference of 3°C. and of 35 per cent. R.H. can produce such a pronounced difference in response, it is clearly of great importance to describe accurately the climatic conditions under which experiments are performed in any behaviour investigation of the type described.

Summary.

Sir Rickard Christophers (1947) working at 25°C. and a relative humidity of 80–90 per cent. found female *Aëdes aegypti* to be attracted by a warm dry surface at 40°C., and to be unaffected by a moist surface at room temperature. The writer (1948), working at 28°C. and 50–70 per cent. R.H. (usually near 50 per cent.) found the opposite : a warm dry surface at temperatures from 36°C. to 40°C. had no effect, while a moist surface at room temperature exerted a quite definite attraction. The purpose of the present experiments was to test the hypothesis that the difference between the results obtained in these two investigations was due to the difference in the ambient temperature and humidity.

Repetition of the relevant experiments at 25°C., 85–90 per cent. R.H., and 28°C., 50–55 per cent. R.H., gave results indicating that temperature and humidity difference operating at the time of the experiment could account for part but not all of the discrepancy. There are indications that the remainder may have been a result of the conditioning effect of temperature and humidity differences operating on the insect prior to the experiment.

The results emphasise the need for a full description of the climatic conditions under which behaviour work of the type discussed is performed.

Acknowledgements.

The work was carried out while the author was on the staff of the Department of Zoology, University of Nottingham, and he is indebted to Professor E. J. W. Barrington, head of the department, for the facilities granted to him.

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ON THE SEX RATIO IN *GLOSSINA*.

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The preponderance of males in tsetse-fly catches has been observed in many species throughout tropical Africa from the earliest days of tsetse research and has excited a good deal of curiosity not only on account of its causes, which are still not thoroughly understood, but because of possible practical and bionomic implications. Thus, according to Fiske's theory (1920) propounded in connection with *Glossina palpalis* (R.-D.) in Uganda, males are generally on the prowl whether hungry or not, and so are readily taken ; females on the contrary are fugitive except when hungry. Moreover, man is not the favourite host ; hence females appear scarce especially when favourite hosts are plentiful. A proportional increase in their numbers indicates a dearth of favourite hosts and consequently greater danger to man who is more liable to attack in these circumstances. Lamborn (1915) points out that pregnant females with good reason seek to avoid males on account of their extreme violence in mating which may result in injury to themselves and their young. This suggests a possible relationship between the sex ratio and the rate of procreation.

The object of this paper is to draw attention to an important factor influencing the proportion of the sexes which appears to have been overlooked : this is, the age of the flies concerned. It is true that Swynnerton (1936) divided some of his catches into young and old flies but this classification did not go far enough ; and Jackson's (1948) admirable studies of the age of tsetse-flies have not, so far as the present writer is aware, been applied to the question of the sex ratio. By means of the simplified system of age-grouping recently proposed by the author (1950), it was shown that flies of the youngest or first age-group have almost consistently a higher proportion of females, *i.e.*, a lower male/female ratio than those in the second and third age-groups. Thus :—

TABLE I.

	A.G.1	A.G.2	A.G.3
Maximum ...	3·4	13·6	8·2
Mean... ...	2·4	5·2	3·5

Subsequent investigations also conducted at Njala from 1st August 1949 to 30th April 1951 confirm these results as will be seen from the following Table :—

TABLE II.

	A.G.1			A.G.2			A.G.3		
	M.	F.	R.	M.	F.	R.	M.	F.	R.
1949									
Aug. ...	130	108	1·2	174	85	2·1	34	29	1·2
Sept. ...	64	50	1·3	76	24	3·2	6	6	1
Oct. ...	144	59	2·5	113	38	3	10	8	1·3
Nov. ...	143	43	3·3	130	51	2·6	31	4	7·8
Dec. ...	—	—	—	—	—	—	—	—	—
1950									
Jan. ...	34	14	2·4	35	13	2·7	3	3	1
Feb. ...	119	30	4	126	37	3·4	18	5	3·6
Mar. ...	505	149	3·4	417	34	12·3	39	12	3·3
Apr. ...	182	77	2·3	264	17	15·5	35	7	5
May ...	204	65	3·1	265	20	13·3	33	1	33
June ...	203	66	3·1	218	18	12·1	23	3	7·7
July ...	141	91	1·5	243	60	4·1	46	18	2·6
Aug. ...	100	70	1·4	205	44	4·7	31	28	1·1
Sept. ...	104	70	1·5	195	31	6·6	32	10	3·2
Oct. ...	126	70	1·8	216	37	5·8	60	18	3·3
Nov. ...	59	40	1·5	83	13	6·4	19	6	3·2
Dec. ...	190	48	4	188	14	13·4	97	19	5·1
1951									
Jan. ...	236	50	4·7	173	18	9·6	62	12	5·2
Feb. ...	284	97	2·9	231	27	8·6	80	21	3·8
Mar. ...	211	62	3·4	270	12	22·5	69	11	6·3
Apr. ...	264	79	3·3	331	26	12·7	99	31	3·2
Totals ...	3,443	1,338	2·6	3,953	619	6·4	827	252	3·3

Evidently, then, females become fugitive whilst in the first age-group. From May to 31st October 1951, A.G.1 was sub-divided into teneral and non-teneral flies. Teneral flies may be defined as those flies with a soft, yielding thorax when held securely between the thumb and index-finger. Doubtful cases were classified as non-teneral. It at once became apparent that the low ratio in A.G.1 is entirely due to the teneral class which is taken in the true natural ratio of unity.

TABLE III.

	A.G.1						A.G.2			A.G.3		
	T.			N.-T.								
	M.	F.	R.	M.	F.	R.	M.	F.	R.	M.	F.	R.
May ...	51	54	0·9	325	25	13	300	22	13·6	28	2	14
June ...	60	62	1	298	37	8·1	204	43	4·7	19	11	1·7
July ...	34	29	1·2	203	44	4·6	131	43	3·0	15	14	1·1
Aug. ...	55	56	1·0	203	81	2·5	208	54	3·9	21	10	2·1
Sept. ...	29	28	1·0	153	36	4·3	101	25	4·0	19	5	3·8
Oct. ...	54	68	0·8	204	55	3·7	193	42	4·6	48	14	3·4
Totals	283	297	1·0	1,386	278	5·0	1,137	229	5·0	150	56	2·7

Non-teneral A.G.1 flies have a similar ratio to that of A.G.2 and an actually higher ratio than that of A.G.3 flies. Females therefore become fugitive at the end of the teneral period, *i.e.*, about seven days after emergence. This is the time when the first egg is approaching maturity, about two days before it passes into the uterus. As this organ lies on the median line in the sixth abdominal segment, *i.e.*, directly under and between the mating cushions, the egg would almost certainly be damaged if the female were mated with the egg in the uterus. While the egg is still in the oviduct it is safe, being then in the fourth or fifth segment according to the stage of development attained.

Teneral females are repeatedly and vigorously mated, copulation on each occasion being prolonged. A female emerging in the laboratory was twice mated on the first day and twice again on the third, the periods *in copulo* totalling two and a quarter hours ; another was covered three times in the first four days of her adult life. It should be stressed that the actual number of matings was probably more than was observed ; moreover, in each case, only one male was admitted. In nature, the teneral females are greatly outnumbered by ardent males of all ages. No time is wasted in courtship. A female is seized in mid-air and violently pummelled with the claspers and one male may be succeeded immediately by another. Thus, although copulation may last for an hour or longer, it is clear that these young females must be very frequently mated. This, no doubt, accounts for the early appearance of the mating scars. It is most unusual to find any but teneral flies unscarred. The teneral stage, then, appears to be the mating phase *par excellence*. It is true that older females are mated, but often only as the result of male importunity, the female " buzzing " the male " off " as if she were an unwilling partner. Renewed mating later in life is evidently necessary in some cases as not all females retain active spermatozoa for life. In the course of investigations at Njala (Squire, 1951), as many as 5 per cent. of A.G.3 scarred (and therefore mated) females showed no spermatozoa on dissection. These females were probably not representative of the wild population.

Under local conditions, the first larva is usually dropped about the 20th day, and succeeding ones at ten-day intervals. By the method of marking, liberating and retrieving, the length of the age-groups was approximately ascertained. A.G.1, *i.e.*, flies with smoky or predominantly smoky wings, comprises flies up to an average of about 32 days old. One fly, 45 days old when retrieved, still qualified for this group. At the other extreme a retrieved fly only 17 days old was classified as A.G.2, *i.e.*, with tawny wings. Unfortunately, only 9 per cent. of released flies were retrieved and most of these too soon to be informative. The following values were, however, obtained for A.G.1 : 45, 42, 40, 32, 30, 30, 21, 17 days. Only one fly was retrieved at the end of the second age-group, *i.e.*, with tawny wings and the first signs of fraying ; it was 85 days old. Assuming this figure to represent the average age at which the fly passes into the third age-group, it will be seen that two larvae may be produced by flies still in A.G.1 and five in A.G.2. It will also be remembered that after each larviposition there is a hiatus of two to three days before the next egg descends into the uterus. Thus, apart from the teneral period of seven days, there are intervals totalling four to six days in A.G.1 and 10 to 15 days in A.G.2 when the uterus will be empty, and when it will be safe for the females to mingle with the males. Assuming A.G.3 to have an average length of 25 days, bringing the total life-span up to 110 days (not an unreasonable assumption), there will then be two more such safe periods amounting to four to six days, making a total during the life of the female of 18 to 30 days. This assumes uninterrupted fecundity which is by no means the case in nature. It is not unusual to find females with neither larvae nor mature eggs yet with active spermatozoa in the spermatheca. Gravid females, too, are fairly safe as it is difficult for the males to clasp them and, in any case, the highly chitinised polypneustic lobes of the third-instar larvae (situated immediately under the mating cushions) are not so liable to damage and consequently the safe periods are probably even longer. This is especially the case in A.G.3, which is probably undergoing a decline in reproductive capacity. Associated with this is the drop in R in A.G.3 observed in Table II. There appears therefore to be some relationship between R and the reproductive capacity of flies in the different age-groups.

There are, of course, other factors influencing the ratio ; at Njala the type of cover in the collecting area is important. It will be noticed that the ratio is generally high in the dry season (December to May) and low in the rains. This was at first thought to be purely seasonal, but it is now clear that it is at least partly due to another factor. In the dry season the fly boys patrol the open river in canoes, a practice which becomes dangerous in the rains ; they then take to the fringing forest where females, and especially older and pregnant females, are more numerous.

Yet another factor is the tendency for females to congregate round cattle, so that it makes all the difference to the ratio whether the flies are taken in the vicinity of a herd of cattle or not. The present writer was privileged to have this demonstrated to him recently by Dr. T. A. M. Nash in the *Isoberlinia* savannah near Kaduna. Some fly boys were catching *G. morsitans* Westw., mostly males, near a party of Africans and Europeans. They were then directed to a small herd of cattle not 50 yards away. Here they took a much higher proportion of females. It may be that females (and especially parturient females) require bovine blood, or it may be that they are merely seeking " safe " hosts. Man and monkeys by reason of their dexterity are unsafe hosts at the best of times, but the danger is greatly increased in the case of gravid females. How much safer they are feeding on the inaccessible belly of the cow ! In the course of investigations at Njala a number of tsetse-flies (*G. palpalis*) were introduced into a cage containing a young Sooty Mangaby, *Cercocebus torquatus atys*, by far the commonest monkey closely associated with the fly in our fringing forests, with the object of observing the fly's method of approach. In a few seconds the monkey had caught and eaten all the flies !

Other factors affecting the flies arise sporadically and can generally be assessed and allowed for, but the age factor is more important because it affects all flies at all times and in all circumstances and, if it is not taken into account, it can obviously vitiate all experiments and observations. Failure to recognize this in the past has probably been responsible for the confusion that has existed.

Summary.

The preponderance of males in tsetse-fly catches is an interesting fact that has not been understood in the past. Attention is drawn to the importance of the age-factor. Teneral flies are nearly always taken in equal numbers whereas non-teneral A.G.1 flies and A.G.2 flies have the highest male/female ratio. In A.G.3, the ratio drops, indicating a decline in reproductive capacity. Females become fugitive about seven days after emergence, at the time when the first egg is almost due to descend into the uterus, *i.e.*, at the end of the teneral stage. This is the mating phase *par excellence*. Mating is prolonged, vigorous, and frequent, and this accounts for the early appearance of the mating scars. As the uterus lies under and between the mating cushions, it is unsafe for females with eggs in the uterus or young larvae to mate. Third-instar larvae are safer as the highly chitinized polypneustic lobes take the brunt of the pummelling from the claspers. Safe periods also occur during the hiatus between larvipositions when the uterus is empty. There are, of course, other factors influencing the ratio, but the age factor is considered paramount, and failure to recognize this in the past has resulted in a good deal of confusion.

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BIOLOGY AND CONTROL OF LABRADOR BLACK FLIES (DIPTERA : SIMULIIDAE).*

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(Plates VIII and IX.)

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The Topography, previous Work, and the Problem.

The principal known requirement for the development of a large population of black flies is an abundance of running, preferably turbulent, water. Mountainous areas with abundant precipitation, or with moderate precipitation and a short season with mean daily temperatures above freezing, provide this. There is much to suggest that the efflux of streams from lakes is also an important favourable factor, probably because of the plentiful development of suitable food micro-organisms in such lakes, and the facility with which gravid flies can locate such sources for oviposition. Over most of Labrador and extensive adjacent areas of northern Quebec, these requirements are ideally provided. Geologically, Labrador is a part of the Canadian Pre-Cambrian shield, and acidic intrusive rocks are exposed in the beds of the streams and rivers and rise to heights above 2,000 ft. over much of the country, especially in the north. The mean daily temperature at Goose Bay, in the south, is below 32°F. for about six months. During the summer running water is abundant, from slow-flowing rivulets in the bogs and muskegs to mountain torrents, and rivers, such as the Hamilton and Naskaupie, punctuated with rapids and falls. Many of these rise from, or flow through, lakes or tarns. The average annual precipitation at Goose Bay is about 28 ins., well distributed throughout the year ; about half of it is in the form of snow.

A further possible requirement for the development of a large black-fly population is the availability of blood meals for adult female flies. Information on the human population, and still more so on the area of Labrador, is conflicting ; it seems unlikely that the mean population density has ever, in recent years, been higher than one person per 25 square miles. This population is largely coastal ; in the interior there is almost none. Some of the more abundant species of black fly appear to prefer man as a host, but even those species that feed on other mammals and birds by preference are not much better off ; their hosts are scarcely more abundant. Yet the populations of black flies that develop in this region are so incredibly great that they have to be seen and experienced to be believed. The writings of all travellers in this region have paid tribute to the "flies" ; the following passages from Packard (1891)are typical:—

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"Our knowledge of the interior of the Labrador peninsula is still so scanty, owing to its inaccessibility, its unnavigable rivers, the shortness of the summer season, and the lack of game, as well as the enormous numbers of black flies and mosquitoes, that any description of this country must long remain imperfect. . . .

"Here we met the black flies in full force, and although we had been fearfully annoyed by them in rambling over Caribou Island, here they were astounding, both for numbers and voracity. . . . The insect finds nowhere in the world such favourable conditions for its increase as in Labrador, over a third of whose surface is given up to ponds and streams. The insides of the windows of Mrs. Chevalier's house swarmed with these fiends, the children's faces and necks were exanthematous with their bites ; the very dogs, great shaggy Newfoundlanders, would run howling into the water and lie down out of their reach, only their noses above the surface. . . ."

Although Packard gives a list of Diptera taken in Labrador, this includes no specific records for the SIMULIIDAE, in spite of their abundance. A reference else-

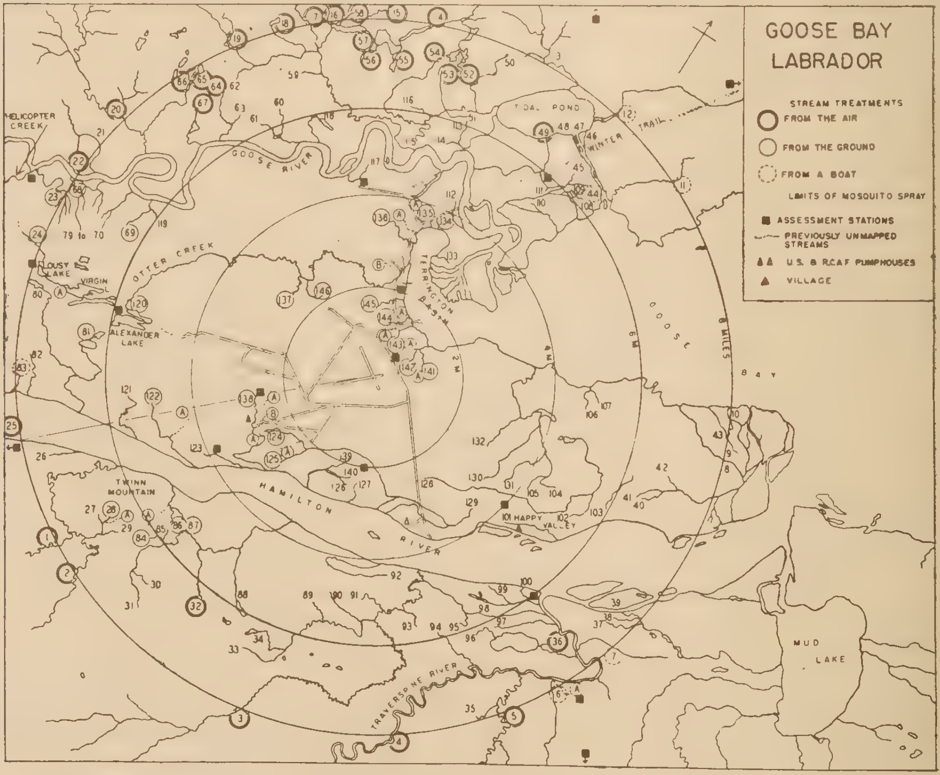
GOOSE BAY
LABRADOR
STREAM TREATMENTS
FROM THE AIR
FROM THE GROUND
FROM A BOAT
LIMITS OF MOSQUITO SPRAY
ASSESSMENT STATIONS
PREVIOUSLY UNMAPPED STREAMS
U.S. & R.C.A.F. PUMPHOUSES
VILLAGE
HELICOPTER CREEK
GOOSE RIVER
TIDAL POND
WINTER TRAIL
OTTER CREEK
LOUSY LAKE
VIRGIN L.
ALEXANDER LAKE
TERRINGTON BASIN
GOOSE BAY
6 MILES
TWINN MOUNTAIN
HAMILTON RIVER
HAPPY VALLEY
MUD LAKE
TRAVERSPINE RIVER

Fig. 1.—Map of the area around Goose Bay, Labrador, showing streams treated and assessment stations.

where in the book to " silvery-legged rascals " suggests that *Simulium venustum* Say was as well represented then as it is today.

The recent establishment of an air base at Goose Bay and the development of plant to work the iron ore deposits along the Labrador-Quebec boundary have focussed attention on this fly pest. The work reported here was done in the vicinity of Goose Bay airport, latitude 53° 20′ N., longitude 60° 24′ W., about 140 miles from the coast, on a peninsula between the points where the Hamilton and Goose rivers empty into Hamilton Inlet. Fig. 1 is a map of the area, and Plates VIII & IX illustrate the nature of the country ; much of it in the south is heavily wooded with spruce and some balsam fir and birch ; dense tangles of alder and willow line the margins of the rivers.

Efficient methods of killing the larvae of northern black flies in running water are now well established (Hocking, Twinn & McDuffie, 1949 ; Hocking, 1950). Recently, Gjullin, Cross and Applewhite (1950) have reported similar results in Alaska, and suggest that overwintered larvae are more resistant to insecticides. Kindler and Regan (1949) reported TDE (1,1-bis (p-chlorophenyl)-2,2-dichloroethane) about five times as toxic as DDT to the larvae of *S. venustum*, giving almost complete mortality at a dosage of 0·5 parts per million-minutes. They also found TDE to be less toxic to fish than DDT, which caused considerable mortality after short exposures at 5 p.p.m. Cope, Gjullin and Storm (1949) recorded observations on the effects of larvicides on both fish and fish food organisms in Alaska, and regarded DDT in fuel oil as among the safer treatments. Vargas (1948) reported a field programme for the control of *Simulium* in relation to onchocerciasis in Mexico. The use of various types of equipment on aircraft has been reported by Wanson, Courtois and Lebied (1949) in the Belgian Congo, and Arnason and others (1949) in Saskatchewan. Helicopter applications have been made in the Adirondacks (Collins, private communication, 1951). A measure of black-fly control may be achieved incidentally in spraying for control of other insects. Goulding and Deonier (1950) reported the control of larvae and emerging adults of *Simulium vittatum* Zett., *S. venustum*, and *Cnephia dacotensis* (D. & S.) during aerial application of DDT at 1 lb. per acre for gypsy moth control. Frost (1949) mentioned the reduction in population of black flies resulting from mosquito control applications of DDT. Aerial spraying operations for the control of adult mosquitos have often included observations of the effect on black-fly populations (Wilson & others, 1949 ; Goldsmith & others, 1949 ; Brown & others, 1951). The results are conflicting but suggest that black flies are not readily killed by this technique and that, if they are killed, the areas so sprayed are rapidly repopulated by infiltration from outside.

Whether the established method of killing black-fly larvae in streams provides the solution to a particular pest problem depends on two conditions : the flight habits of the important species and the distribution of breeding sites. In spite of an apparent flight range of 100 miles or more, *Simulium arcticum* Malloch can be controlled in this manner in Saskatchewan owing to its limited breeding sites. It appears that *Simulium neavei* Roubaud and *Simulium damnosum* Theo., in spite of their extensive breeding areas in Africa, can also be controlled in this manner because of their restricted flight range, although Gibbins (1934) has suggested that *S. damnosum* flies distances up to 30 miles, and Wanson (1950) considers this species capable of flying 35 miles through favourable country. Dalmat (1951) showed experimentally that *Simulium metallicum* Bellardi, an onchocerciasis vector in Guatemala, flies at least 7·4 miles, and recorded one female flying 3·8 miles in one day.

There is little information on the flight habits of the species important in Labrador, and, although many of them are believed normally to remain close to the streams in which they developed, their large numbers would probably provide a strong stimulus to migration into an area cleared of flies by control measures. Because destruction of the larval stage permits a much larger area to be covered than aerial spraying against adults, this method was selected for an experimental control project around Goose Bay, and the project was designed to provide indirect information on these important flight habits. A preliminary survey of the area around the airport was made during the summer of 1949. This was to determine what species were present, which of them were important pests of man, where the principal breeding sites of these were situated, and on what dates they pupated and emerged. The control experiment itself was carried out in 1950. Results were somewhat complicated by applications of DDT in oil solution from the air for control of mosquitos, in the larval stage in 1949 (Twinn, Brown & Hurtig, 1950), and as adults in 1950 (Brown & others, 1951). In 1949 applications were made selectively to areas where mosquito breeding was heavy. With the exception of bog streams to the north-east of Lake Alexander, the effect on black-fly larvae was slight. The average application rate in 1950 was 0·165 lb. of DDT per acre as a 4·2 per cent. solution in oil ; the area over which this was applied was 18·7 square miles and is marked with a dotted line in fig. 1. Applications were made between 28th June and 2nd July, when black-fly emergence had not long begun.

TABLE I.

Described species of black flies recorded in Labrador, dates of earliest pupae, and period of adult activity. Goose Bay, 1949 and 1950.

Species	Earliest pupa	Water temp. °F.	Approx. degree-days over 32°F.	Stream nos.	Period of adult activity	% in cloud attacking man (1950)
Simulium venustum Say	13.vi.	52	304	4, 20, 22, 24, 25, 120	18.vi.–5.ix.	93·1
S. perissum D. & S. ...	13.vi.	52	304	4, 24, 25, 120, 136, 138	16.vi.–5.ix.	0·8
S. corbis Twinn ...	16.vi.	50	370	4	7.vii.–18.viii.	0·2
S. pictipes Hagen ...	28.vii.	54	1,474	22, 25	No record	0
S. decorum Wlk. ...	15.vi.	55	350	24, 136	19.vi.–18.viii.	1·2
S. vittatum Zett. ...	7.vi.	—	201	5, 120	12.vi.–	<0·1
S. rugglesi Nicholson & Mickel	No record	—	—	138 ? 143 ?	12.viii.–13.viii.	0
S. parnassum Mall. ...	No record	—	—	22 ?	7.viii.–16.viii.	0·1
Prosimulium hirtipes (Fries)	22.vi.	43	517	120, 138, 144	25.vi.–20.viii.	4·4
P. multidentatum (Twinn)	11.vi.	40	267	145	No record	0
P. browni (Twinn) ...	22.vi.	48	517	145	25.vi.–26.viii.	0
Eusimulium aureum (Fries)	10.vii.	—	—	135A	26.vii.–	<0·1
E. pugetense D. & S. ...	18.v.	33	58	4, 120, 138, 143, 144		<0·1
E. euryadminiculum Davies	7.vii.	—	884	120	—	0
E. latipes (Mg.) ...	18.vi.	68	428	24, 136	19.vi.–13.viii.	0
E. croxtoni Nicholson & Mickel	18.vi.	68	428	Bog streams	—	0
Cnephia dacotensis (D. & S.)	19.vi.	65	460	136	19.vi.–	0
C. mutata (Malloch) ...	9.vii.	—	935	138	9.vii.–5.viii.	<0·1
Gymnopais holopticus Stone...	24.viii.	45	1,980	—	—	0

The Species present and their Biology.

During the 1949 season, samples of larvae and pupae were collected periodically from what appeared likely to be the more important black-fly breeding streams and rivers near Goose Bay. Larvae were preserved and pupae taken alive for rearing on moist filter paper in petri dishes, to secure adults associated with pupal skins and cocoons. Samples of adults were also taken periodically in the field, by sweeping with a 12-in. net in the cloud that collected around the observer. These observations were supplemented by a method described by Ide (1940), cages of 24-mesh plastic screening to cover a square yard of stream bottom being placed in two of the more interesting streams. Male and female flies emerging into these cages were collected at intervals. Several estimates of the adult population density at various places were made during the season.

A list of all the described black-fly species now recorded from Labrador is given in Table I, together with a summary of their seasonal appearance, distribution, and relative abundance. In addition to these, six undescribed species have been recorded, four in the genus *Eusimulium* (one of them *Eusimulium* sp. B. of Twinn & others, 1948), and one each in the genera *Cnephia* (near *pecuarum* (Riley)), and *Gymnopais*.

In 1949, when most of this information was recorded, the season opened later than usual ; the mean temperature for May was five degrees below the long-term average of 39·8°F. June was a little warmer than usual, but July was cooler. The planning of control work in 1950 was upset by the fact that the season opened unusually early ; the average temperature for the last ten days of April was 39·2°F., that for May 42°F., and that for June 53°F., as compared with a long-term average of 50·5°F. Snowfall in the winter of 1949–50 and rainfall in May and June 1950 were heavier than usual, favouring a large population of black flies.

The principal areas investigated in 1949 are described below, in the sequence in which black-fly development was discovered in them ; numbers in brackets refer to fig. 1. Notes on the species follow these descriptions.

1. *South Terrington stream* (144), 18.v.—This stream is about three-quarters of a mile long, has its origin in a small swamp, and flows into Terrington Basin. It is a typical forest stream, with muck bottom except for a short gravel stretch near the road culvert. The flow was about 1 cusec. Well-developed larvae were found at an average density of about three to a rock for a distance of 20 yards. The water temperature was 33°F. and much of the surrounding forest was still under snow. Adults emerging in the insectary on 1st June from pupae later collected here proved to be of *Eusimulium pugetense*. Pupae of *Prosimulium hirtipes* were also collected here, on 22nd June. Mid-Terrington stream (145), 1,000 yards to the north, has similar characteristics.

2. *American Pumphouse stream* (138), 23.v.—This stream runs in a steep-sided little valley three miles south of the airport, and empties into the Hamilton River. Above the pumping station it is clear, 3–4 ft. deep, and swift. The bed is of silt and white sand, the edges thickly grown with moss, and the whole covered for much of its length with a dense tangle of deadfall. The infestation was heavy, up to 20 larvae per square inch being found on some of the submerged logs. The species present were *E. pugetense* and *P. hirtipes* ; in 1950 an unidentified species of *Gymnopais* was found here.

3. *Otter Creek* (120), 3.vi.—This has its origin from Lake Alexander, flows for eight miles mainly through bog country, the banks densely grown with alder and willow, and empties into Terrington Basin. The water is a brownish-red. Submerged twigs throughout the length of the creek each carried two or three larvae. The species collected here were *P. hirtipes* and *Prosimulium browni* ; *E. pugetense* was taken here in 1950.

4. *Helicopter Creek*, 17.vi.—This flows into Goose River nine miles west of the airport. There is an extensive system of rapids and a heavy flow. The bed is of rocks and boulders, with some clay. During June the infestation was slight, but by 5th August there were two or three larvae to every small rock. Species taken here were *Simulium venustum*, *S. perissum*, *Prosimulium multidentatum* and *P. hirtipes*.

5. *Goose River* (22), 23.vi.—This is the second largest river in the area. It is 75 to 100 yards in width and has a very variable flow, up to 3,000 cusecs. The river bed is of fine sand and gravel ; there are rocky rapids about 12 miles above the mouth. Infestation was moderate apart from that at the rapids, but very general, extending at least 18 miles. The rapids have a length of 200 yards, with a fall of 15 to 20 ft. ; the igneous rocks here were all heavily laden with larvae, over 400 being counted on one area 6 ins. square. The principal species were *Simulium pictipes*, *S. venustum* and *S. perissum*. This river is an important source of black flies.

6. *Traverspine River* (4), 16.vi.—Rather smaller than the Goose River, this flows through heavily wooded country, entering the Hamilton on the right bank, six miles above its mouth. The water is deep brown and the bottom is of rock and sand. About five miles up the river is a series of rapids, of which the first is 500 yards long. All of these contained some black-fly larvae, but not heavy infestations. *E. pugetense*, *Simulium corbis*, *S. venustum* and *S. perissum* were found here.

7. *Bog streams*, 18.vi.—These are an assemblage of small streams draining the bog areas to the north-east of Lake Alexander. They are not more than 1 ft. wide and 2 ft. deep, the sides heavily grown with sedges and moss. As breeding areas they are not important individually, but together they probably make a significant contribution to the abundant black-fly population in the bogs in July and August. *Cnephia dacotensis*, *Eusimulium latipes*, *E. croxtoni* and *Simulium decorum* were taken here.

8. *Hamilton River* (25), 28.vii.—This impressive river, nearly a mile wide, flows from west to east some three miles south of the airport. Here it has a shifting sand bed, with much gravel along the shore lines, and several islands and sand bars. Black-fly larvae infest its margins extensively, as far up as Muskrat Falls, 18 miles above the airport, and presumably beyond. Muskrat Falls are about 200 yards wide ; the lower falls are 30 ft. high and the upper falls 40 ft. It was not possible to examine the full width of the river here, but the rocks on either side and the small offshoots of the main stream were all heavily infested with larvae. *S. pictipes* was taken here ; elsewhere in the Hamilton River, *S. venustum* and *S. perissum* were common. Pupae of *Gymnopais holopticus* were taken from a stream flowing into the Hamilton from the south about two miles above the falls.

9. *Area north of Goose River*, 31.vii.—A section of this rather inaccessible area was examined. The steep rocky hills are nearly 1,000 ft. high and are interspersed with deep valleys wooded heavily with spruce and balsam fir. In the valleys are spring-fed streams, with an average temperature at this time of 41°F. These run over rocky beds and are bordered by very dense willow and alder growth which is a serious impediment to travel. Every stream visited in this area contained many black-fly larvae ; very few pupae were found, and these were of *E. pugetense*. Adult flies here at this time were the most abundant experienced during the 1949 season ; they were mainly *S. venustum*, but specimens of *S. decorum*, *S. corbis*, *S. perissum*, and *P. hirtipes* were also taken.

The black-fly species recorded in Labrador may be divided into two groups according to their blood-sucking habits. A number of species are not found in the swarms attracted to man. In this group are the two species of *Gymnopais*, *Cnephia dacotensis* and the undescribed species of *Cnephia*, *Eusimulium latipes*, *E. euryadminiculum*, *E. croxtoni* and the two undescribed species of *Eusimulium*, *Prosimulium browni* and *P. multidentatum*, and *Simulium pictipes*. Borderline species which should perhaps be included in this group, only rarely attracted to man, are *Cnephia mutata, Eusimulium aureum, E. pugetense* and two undescribed species of *Eusimulium*, and *Simulium rugglesi*. Of the remaining species, *S. venustum* and *P. hirtipes* may be regarded as important biters of man ; and *Simulium vittatum, S. perissum, S. decorum, S. corbis* and *S. parnassum* are also attracted to, and probably bite, man.

The species may also be subdivided on differences in the life-histories. On this basis, larvae of one group, *E. pugetense, P. hirtipes, P. browni*, and *P. multidentatum*, are to be found in most of the small forest streams, and in rather larger streams while they are in flood. Pupation of this group generally occurs by the time the water temperature reaches 50°F. These four species appear to overwinter in the larval stage, since well-grown larvae can be found early in May, when parts of some of the streams are still covered by several feet of snow. Figures for degree-days for these species in Table I represent the cumulative temperature required to complete development in the spring, not to develop from the egg. Streams containing principally these species, such as Otter Creek and the Pumphouse stream, were found to be reinfested with young larvae late in August. None of these species was found in either the Goose or the Hamilton River.

The remaining species occur in bog rivulets, or in the larger streams and rivers after flood conditions have abated, larvae usually making their appearance when the water temperature rises above 45°F. The presence of pupae late in the season, and of small larvae in midsummer, suggests that none of these species normally overwinters as larvae or pupae. The only important species for which there is evidence of more than one generation a year at Goose Bay is *S. venustum* ; succeeding generations are not well defined but have the effect of building up the adult population late in the season ; this species reaches a peak of abundance about the middle of August. This is by far the most numerous and troublesome species, and may continue active well into September.

P. hirtipes is normally the first of the pests of man to appear on the wing, but from early July onwards it takes second place to *S. venustum*. Minor species appearing with *S. venustum* are, in order of importance : *S. decorum, S. perissum* and *S. corbis*. Collectively, through the season as a whole, these three species are less important than *P. hirtipes*.

Two methods were used in 1949 to obtain an approximate idea of the abundance of black flies. The first of these, the *landing rate*, is a count of the number of flies landing on the front of the trousers between the waist and the knee during one minute, while facing halfway between down-wind and away from the sun. The second, the *sweep count*, is the number of flies taken in a certain number of sweeps, usually a multiple of ten, with a 12-in. net held at arm's length. The sweeps were made in the cloud of flies attracted about the observer, without striking vegetation.

In 1949, during the latter part of June and early July landing rates in the forests and bogs around the airport rarely exceeded 25. The earliest records of large numbers of black flies were obtained in the area north of Goose River. On 25th July landing rates of over 150, and sweep counts of over 300 specimens in 30 sweeps, were recorded here. By 8th August similar conditions occurred to the south of Goose River, and by 15th August, landing rates over 60 were recorded at the base of the slopes of the plateau on which the airport is situated. The top of this plateau, which is mainly open country, was relatively free from flies until nearly the end of July. Complaints of biting there became more numerous after 20th July, children and sun-bathers being the chief victims ; landing rates of 7 were recorded in the open, on 15th August.

The two emergence cages already described were set up in the Pumphouse stream on 5th July. The water temperature varied little, the average maximum being 46°F. and the average minimum 40°F. The highest temperature was 51°F., on

TABLE II.

Black-fly emergences in cages, American Pumphouse stream, Goose Bay, Labrador, 1949.

Date	*P. hirtipes*		*C. mutata*		*E. pugetense*		*S. perissum*		*S. venustum*		Total
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	
30.vi. ...						1				1	2
2.vii. ...		1				1				4	6
6.vii. ...		1				4					5
7.vii. ...						1					1
8.vii. ...		2			2	3					7
9.vii. ...	1	1		2	2	3					9
11.vii. ...	64	47			1	5		11		6	134
13.vii. ...	3	1		1				1		1	7
15.vii. ...	5	1									6
18.vii. ...	10	1						2		16	29
19.vii. ...	4	2						3		3	12
20.vii. ...	2	1									3
21.vii. ...	19	5								1	25
24.vii. ...											0
25.vii. ...	18	6	1			2					27
26.vii. ...	10	7		1						1	19
30.vii. ...	24	15				1				8	48
4.viii. ...	48	25		1		2					76
6.viii. ...	23	18									41
11.viii. ...											0
18.viii. ...	12	10									22
19.viii. ...	10	34									44
Total ...	253	178	1	5	5	23		17		41	523

13th July, and the lowest 39°F., on 25th July. Table II summarises the data obtained from these cages. Flies emerging into the cages were collected at intervals by the observer, who entered the cage for this purpose. This allowed the entry of some female flies from outside, and the fact that no males of *S. venustum* or *S. perissum* were recorded suggests that these 2 species were not breeding in the stream.

On 17th June 1950, during the survey before treatment of streams, a most remarkable concentration of black-fly larvae was found at the efflux of stream 24 from the north end of Lousy Lake, which owes this name to the infestation. This stream originates from the west end of Virgin Lake, and flows into Lousy Lake from the south and out from the north, the reverse direction to that indicated on maps. A moderate infestation was found in the stream between the two lakes, but in the first 10 yards of the stream flowing from Lousy Lake it was estimated that there were more than a million larvae, most of them approaching maturity, and a considerable portion harbouring mermithid parasites. Among the pupae collected were *S. venustum*, *S. perissum*, *S. decorum* and *E. latipes*. The width of the stream at this point was 15 feet ; fallen branches interlaced with the living stems of alders formed a natural dam at the outlet of the lake ; on the twigs of these plants, and on the abundant sedges at the margins of the streams, the larvae were clustered so thickly that it seemed impossible to add to their number.

An Experiment in Area Control.

It was at first proposed to eliminate black-fly larvae from streams and rivers within a radius of 10 miles of the intersection of the runways at the airport, before pupation had commenced, and then to study the process of infiltration into this cleared area by flies emerging from larval habitats outside. The lack of large-scale maps for areas beyond 8 miles to the north and west, together with the very large number of streams and the difficulty of travel, forced a reduction in the radius treated to 8 miles, an area of 200 square miles.

Initial survey.

An 8-in. circle was drawn on a 1 inch to the mile map of the area, with the intersection of the main runways at the airport as centre (fig. 1). This area was then subdivided by drawing additional circles with radii of 2, 4 and 6 in., and a radius to the intersection of the 8-in. circle with a right bank of the Hamilton River. Streams shown on this map were then numbered in sequence as follows : (*a*) streams flowing into the area from outside, anticlockwise around the 8-in. circle starting at the drawn radius ; (*b*) streams arising within the area between the 8-in. and 6-in. circles, anticlockwise starting from the drawn radius ; (*c*) similarly for streams arising between the remaining circles and within the 2-in. circle. This procedure gave a total of 146 mapped streams and rivers to be investigated and, if necessary, treated. During this work 17 unmapped streams were located and given the numbers of the nearest mapped streams plus the letters A or B, making a total of 163 streams and rivers.

Work on surveying these streams was begun at the end of May. The survey was intended to establish the existence of the streams as mapped ; their general suitability for black-fly larvae as regards turbulence, turbidity and source, and especially the flow of water in the suitable streams on which to base calculations of the quantities of material required for the treatments. Observations on the prevalence of black-fly larvae were made when possible, but as it was often easier to treat a stream than to decide whether treatment was needed, suitable streams were treated regardless of whether the presence of larvae had been established. A Sikorsky, type H 5G, helicopter proved of great value in the survey. The width and the speed of flow of streams can be estimated with reasonable accuracy from a helicopter ; when the sun is shining the shadow of the aircraft is a useful yardstick. The estimation of depth is possible only if the water is reasonably clear. When this is so, if allowance is made for the apparent reduction by refraction, it is usually possible to obtain a reasonable estimate of mean depth. The flow in several streams was estimated from the air, and later checked on the ground. Except for turbid streams the results agreed within 10 per cent.

After a week of survey work, prevailing high temperatures made it advisable to commence treatments if these were to be completed before pupation became general. Survey and treatment were then conducted concurrently.

The survey showed that 86 of the streams required no treatment because they had dried up or had little or no flow. Some of the forest streams were subterranean for a considerable portion of their length, having been grown over by moss and the roots of trees. These presented some difficulties ; they could be followed on the ground by listening for them and by watching for stream vegetation, but were difficult to examine for larvae and almost impossible to see and treat from the air. Larvae were frequently found in such streams, but never in the subterranean portions, except downstream of exposed stretches.

No larvae were found in any of the streams in the flat, low-lying peninsula east of the airport, most of which were dry. There were almost none in the Goose River delta, in the area between Goose Bay and the winter trail to Northwest River, and in the sluggish streams flowing through the boggy area between the Hamilton and the Traverspine rivers. The most important larval habitats are the streams north of Goose River and west of Tidal Pond, the streams draining from the Alexander Lake and the Lousy Lake system, and the streams draining from Twinn Mountain and the mountains south and west of this.

Insecticidal treatments of streams.

The original intention was to treat by ground application all streams and rivers that could be conveniently reached on the ground, and then to complete the treatments from the helicopter. Partly because of maintenance difficulties with the helicopter, but more because of the difficulty of reaching suitable sections of some of the streams owing to the steep-sided, densely wooded valleys, it proved necessary to treat from the helicopter those streams that could conveniently be so treated, and by some other means to reach the remainder on the ground.

All treatments except those of the Hamilton and Goose rivers, which are described later, were made with a 10 per cent. solution of DDT in fuel oil and an auxiliary solvent. The dosage desired for all streams was 1 part of DDT in 10 million parts of water for 15 mins., or 1·5 p.p.m.-mins. When treating from the helicopter, however, it was necessary to reduce the time, often to as little as 3 mins., and to increase the concentration in proportion. This was because of the difficulty of hovering over many of the streams at a height of 40 ft. or more necessitated by the presence of trees or steep banks. This was offset to some extent by the fact that many streams were treated by helicopter at their efflux from lakes, where the gradual feeding of lake water into the stream extended the exposure time.

Twenty-seven of the 77 streams were treated from the helicopter, 42 from the ground, and seven from boats ; one, the Hamilton River, was treated from a Dakota (C47) aircraft. In the initial arrangement used in the helicopter, a 30-ft. length of ½-in. rubber hose was attached to the outlet of a larvicide dispenser (Hocking, 1950). The hose was lowered through the door for applications, its lower end weighted with a 6-ft. length of ½-in. iron pipe. This arrangement was necessary to prevent the break-up and dispersal of the insecticide by the down-draught from the rotor. The heavy, stiff rubber hose was very awkward to manipulate in the cabin of the aircraft ; a lighter and more flexible plastic hose, with a simple winch to lower and raise it, would be necessary for the regular use of this equipment. A wooden platform was used to bring the level of the floor of the left side of the aircraft cabin up to that of the doorstep and the control conduit in the centre. This facilitated movement of the dispenser to get the outlet pipe through the door for treatments ; the equipment should, however, be fixed into the aircraft. This dispenser was intended for all applications from the helicopter or boats, but it fell from the helicopter into an inaccessible bog on 13th June. Thereafter, the insecticide was measured out and dribbled into a funnel at the top of the hose.

From the ground and from boats, insecticide was dribbled directly into the stream. To eliminate hovering, and the flying time consumed in this, the possibility of applying treatments by a briquette method, as tested by Fairchild and Barreda (1945), Prévost (1947) and Raley and Davis (1949), was considered. Suitably standardised, such a method might prove invaluable. Hitherto, however, this method has been uncertain as to dosage and time of exposure. Two small streams (137 and 146) were treated experimentally from the ground by dropping into them muslin bags containing local sand passed through a 20-mesh screen, into which the measured amount of DDT in oil solution had been absorbed. Control was effected in these instances, although 36 hours later much of the oil solution was still present in the sand bag. The rates of flow where the bag was immersed were 1·5 and 1·3 feet per second.

The procedure adopted with helicopter treatments was to locate the stream near its mouth from a height of 100–200 ft., and to follow it upstream in search of a suitable place at which to apply insecticide. Flow and dosage calculations were made while this was being done. It was helpful to have a navigator to direct the pilot to the streams and to record the treatment sites on a map. It was never possible to get down to the surface of the stream exactly at the point where it entered the 8-mile circle, and most of the streams had to be treated some distance, sometimes several miles, outside the treatment circle. In this experiment it was obviously undesirable to eliminate larvae beyond the treatment area ; few streams, however, carried the insecticide out of the area on the downstream side, because of the topography. Most of them emptied directly or indirectly into Goose Bay within the treatment circle.

Treatment of the Hamilton River by Dakota also had to be done outside the area, namely, above Muskrat Falls. This was partly because there was little turbulence below this point to distribute the insecticide, and partly because the height of the banks below the falls made low flying difficult. This treatment was made between 11.00 and 12.00 hrs. on 20th June ; the plane flew six circuits, crossing the river obliquely just above the falls on a ½-mile track at a height of 30 ft. above the banks. A 15·4 per cent. solution of DDT in fuel oil and auxiliary solvent, dyed with Dupont oil red, was discharged by gravity flow through a straight emission pipe (Twinn & others, 1950) for 15 secs. on each circuit. Each circuit took 2·5 mins., so that the whole application occupied 15 mins., during which time 403 lb. of DDT were applied. The flow in the river at this time was 72,000 cusecs, so that this gave an average concentration of 0·1 p.p.m. The sky was overcast and atmospheric conditions were stable. The spray could be seen settling on the water, and the foam

TABLE III.

Summary of data on insecticidal treatment of black-fly streams. Goose Bay, 1950.

Date	Streams treated			Total flow in cusecs	Total DDT used, cc. of 10% solution
	From the ground	From the air	From boats		
7.vi.	135A, 136, 136A, 141, 141A, 142, 142A, 143, 143A, 144, 145, 145A, 145B			4·2	106·8
10.vi.	86, 87 ...			4·5	114·7
12.vi.	124A, 138, 138A, 138B			5·5	140
13.vi.	134, 135	1, 2, 4, 5, 36		114·1	2,916·2
14.vi.	146	3, 32, 49		40·0	1,020
16.vi.	137			0·2	6·1
17.vi.	24, 24A, 120			83·5	2,130
20.vi.		14 to 20, 52 to 58, 64 to 67		341	8,710
20.vi.		25 from Dakota aircraft		72,000	*$1{\cdot}835 \times 10^6$
21.vi.	122, 122A, 124, 125, 125A			28·2	720
22.vi.			11, 12, 44	56·1	1,430
24.vi.			83	0·8	21
25.vi.			6, 6A, 7	10·9	278
26.vi.		22		2,900	*$7{\cdot}4 \times 10^4$
26.vi.	23, 68, 73, 76			1·4	34·5
27.vi.	69, 71			4·3	110
28.vi.	81			5·3	136
29.vi.	28, 28A, 84, 86A			8·2	210
Total numbers treated	42	28	7		
Total 10% DDT solution used (Imperial gallons)				Approx. 425	

*Applied at higher strength ; the equivalent of this volume of 10% solution was used.

of the falls was tinted pink as it passed through them. No larvae could be found when the falls and other stretches of the river were examined on 24th June. A similar solution was used in treating the Goose River from the helicopter. The 30-ft. hose was coupled through a valve to a 10-gal. drum containing the insecticide, which was again emitted by gravity flow.

Treatments were completed by the end of June, occupying about 400 arduous man-hours. Pupae of the earlier species could be found a few days before this. A chronological summary of the treatments of the streams is given in Table III. Whenever possible, confirmation of the effectiveness of a treatment was obtained by re-examination 24 hours or more afterwards. This could not be done often, but the co-operation of other entomologists working in the area was obtained in searching for remaining larvae during July. Until some of the streams became reinfested with young larvae early in August, the only larvae found within the treated area after 30th June were in a 40-ft. stretch of slowly running water that had been overlooked ; it drained from an old ox-bow into the Goose River near the winter trail. Large numbers of larvae and pupae of *S. venustum*, and some of *E. aureum*, were found here on 10th July. A few days later the level of the water had dropped and most of the infestation had disappeared. A few feet near the source of each of the streams in which emergence cages were placed were left untreated, and a few larvae persisted at these places. No other larvae were known to survive, although, in an area of this size and complexity, it is probable that some minor infestations remained undiscovered.

Assessment of the effect of treatments.

Absolute estimates of the population density of black flies are difficult to obtain, the mere presence of an observer having a profound influence on the population, an influence to which the attention of the observer is inevitably directed. In attempting to obtain such estimates the following procedure was adopted. The counts already referred to as *landing rate* and *sweep count* were used in a somewhat more refined form ; specific sites were defined at which these were taken. For the landing rate, the fabric of the trousers was recorded, and the area observed was defined as that between the side seams from waist to knee ; no attempt was made to recognise individual flies, and if a fly landed twice, this was counted as two landings. In the sweep counts, ten single sweeps were taken across the front of the body, the net was closed immediately after the last sweep, and the end was put into a large jar with a chloroformed plug at the bottom. As soon as the flies were inactive they were placed on a white card, counted, and transferred to a labelled vial of alcohol-glycerine preservative. These counts were supplemented by a measurement of biting activity. The biting rate used for mosquitos is not suitable for black flies, as the latter are much slower to bite and the reactions to their bites may be serious enough to limit the number of observations that an individual can take. Instead, a forearm was exposed from wrist to elbow, and the time recorded to the first penetration. A maximum of 5 mins. was allowed.

An attempt was made to use a measurement less influenced by the observer, by exposing screens coated with adhesive ; variously coloured solid screens and meshes of various sizes proved unattractive to the flies, so that impracticably large screens would have been needed to secure a useful number of captives.

Assessment records were taken as opportunity offered at points outside the treatment circle, and as nearly as possible twice weekly, at each of the ten sites selected within the circle, as follows :—

Near the 6-mile circle :—
  6A, Lake Alexander, N.W. shore ;
  6B, winter trail, crossing of stream 49 ;
  6C, mouth of the Traverspine River.

Near the 4-mile circle :—
  4A, near the mouth of the Pumphouse stream;
  4B, Goose River, near stream 117 ;
  4C, Happy Valley, near stream 101.

Near the 2-mile circle :—
  2A, near the source of the Pumphouse stream ;
  2B, Otter Creek, near the road bridge ;
  2C, Old Farm area, near stream 140.

Near the centre : the nearest sheltered situation to the centre of the circle, in the forest at the foot of the slope from the airport plateau, near the source of stream 142.

The sites were chosen to give the most favourable conditions for black-fly adults, with a sheltered aspect and generous vegetation. At each site three points about 15 yards apart and arranged in a triangle were selected and marked. On arrival at a site, wet- and dry-bulb thermometer readings, the extent of cloudiness in tenths, and the approximate wind speed were recorded, and the time of day was noted. The biological observations were not begun until at least three minutes had elapsed after arrival, to allow time for the flies to gather. With few exceptions all observations were made between 10.00 hours and 16.00 hours to avoid interference from the diurnal rhythm of activity.

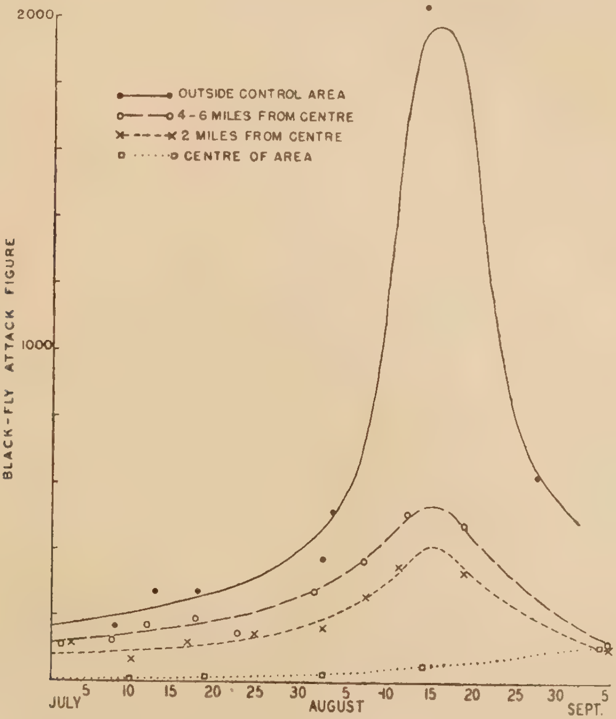

Fig. 2.—Intensity of black-fly attack plotted against time. Goose Bay, Labrador.

Several observers made biological assessments and, although parallel sets of observations were often made by two or more men, insufficient data were obtained for corrections for personal variation in attractiveness to be applied. However, at least three observers made records at each site at some time during the season.

When more than one observer visited a site at the same time, each observer took biological readings at each of the three points. The other principal factors influencing the figures obtained were the clothing worn, especially its reflectivity, and weather conditions, the former having little influence except on the landing rate. Corrections for these two factors were applied as indicated in the following paragraphs.

Davies (1951) showed how the landing rates of black flies on coloured cloths vary with reflectivity for sunlight and for ultra-violet radiation. To enable corrections on the basis of these figures to be applied, the reflectance ratio by comparison with a black fabric was measured for the materials of which the observers' trousers were made. This was done in sunlight, by means of a Weston model 715 photographic exposure meter. To measure the reflectance ratio for ultra-violet radiation a 275-watt mercury arc sunlamp transmitting to 2,800 A.U. with a peak at 3,300 was used in conjunction with an R.C.A. No. 935 photocell shielded with a 1-cm. Corning red-purple Corex filter, transmitting from 4,000 A.U. These measurements, and the expected landing percentages as compared with 100 per cent. on a black fabric, derived from them with the aid of Davies' figures, are given in Table IV. Of the materials tested, that of the R.C.A.F. uniform proved much the most attractive.

TABLE IV.

Reflectivity of clothing fabrics, and expected black-fly landing percentages.

	Sunlight reflectance ratio (colour/black)	U/V reflectance ratio (colour/black)	Expected landing percentage (black, 100)
Blue denim	2·2	1·2	74
Khaki nylon	14·7	4·6	34
Green nylon	4·4	2·3	58
R.C.A.F. blue serge	1·5	0·85	92
Khaki drill	11·8	2·6	36

Corrections for variations in temperature and in saturation deficiency were also derived from data compiled by Davies (private communication, 1949). These three corrections were then applied as indicated in the next paragraph.

The principal results of the experiment are embodied in fig. 2, in which a composite black-fly attack figure is plotted separately against time for points outside the area and on the 8-mile circle, for points on the 6- and 4-mile circles, for points on the 2-mile circle, and for the central assessment site. The black-fly attack figures were calculated from the following expression :—

$$\text{Attack figure} = f_t f_s\left(a+\frac{f_c b}{2}+\frac{100-x+y+z}{9}\right)$$

where f_t, f_s, and f_c are the correction factors for temperature, saturation deficiency, and clothing colour, respectively, a is the total sweep number from the three points, b the total landing rate for the three points, and x, y, and z the times to the first bite at each of the three points. The divisors 2 and 9 were used to balance the weight attached to each of the three sets of observations.

The effect of applying these corrections was to give much better agreement between the figures obtained by different observers at the same time and site (f_c), and a much more uniform trend in the sequence of figures obtained by a particular observer at a particular site. There remained, however, a few sets of readings that were aberrant ; on the occasions of all such readings there was a rapid change in barometric pressure, often with high winds, or there was almost no wind ; on one occasion of high figures there was much thunder. No arithmetical corrections for these conditions could be applied, but allowance was made for them in drawing the curves. The curves were drawn from 5-day running averages of these attack figures for each zone ; for the sake of clarity only selected points are marked in. Data for sites outside the control area were not so complete as for those nearer the centre. The helicopter was not available at this time, and there were other obstacles to transportation. The highest figures recorded at any time and place were at Grand Lake, 26 miles N.N.W. of the centre of the area, on 14th August, when uncorrected landing rates were above 200, and three sets of ten sweeps yielded as many as 1,705 black flies. The average time to the first bite on a forearm was 43 seconds. This was one of the few sites where readings were obtained well beyond any stream treatments.

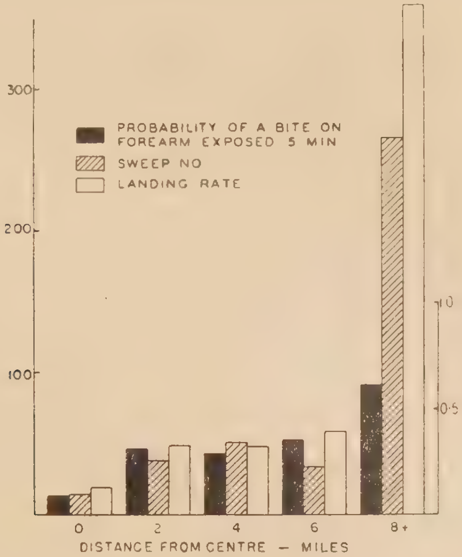

Fig. 3.—The effect of black-fly control measures in the Goose Bay, Labrador, area. Uncorrected seasonal averages.

Fig. 3 records the uncorrected seasonal averages of sweep numbers (totals for three sets of ten sweeps) and landing rates (totals for three points), and the probability of a bite being obtained on a forearm exposed for five minutes, at each of the five assessment zones. Averages were taken over the whole of the period for which observations were made, from 1st July until 5th September.

In fig. 4, the percentages of *S. venustum* and of *P. hirtipes* in the population attacking man are plotted against time for each of the four zones used in fig. 2. These are the only two species that were present in sufficient numbers for this procedure to yield useful information. *P. hirtipes*, with only a single generation, normally decreases in abundance rapidly as the season advances. A few other features of the species distribution in sweep samples are of interest. In two samples *S. decorum* was present in striking abundance ; on 13th July at Helicopter Creek, 32 out of 103 specimens were of this species, and on 4th July at Traverspine River there were seven of *S. decorum* out of 50 specimens. Since the over-all occurrence of this species in the sweeps was only 1·2 per cent., this suggests very localised larval habitats and very limited flight habits for this species. Only one of the samples taken at the centre site contained specimens of any species other than *S. venustum* ; on 14th August four out of 18 specimens were *S. perissum*.

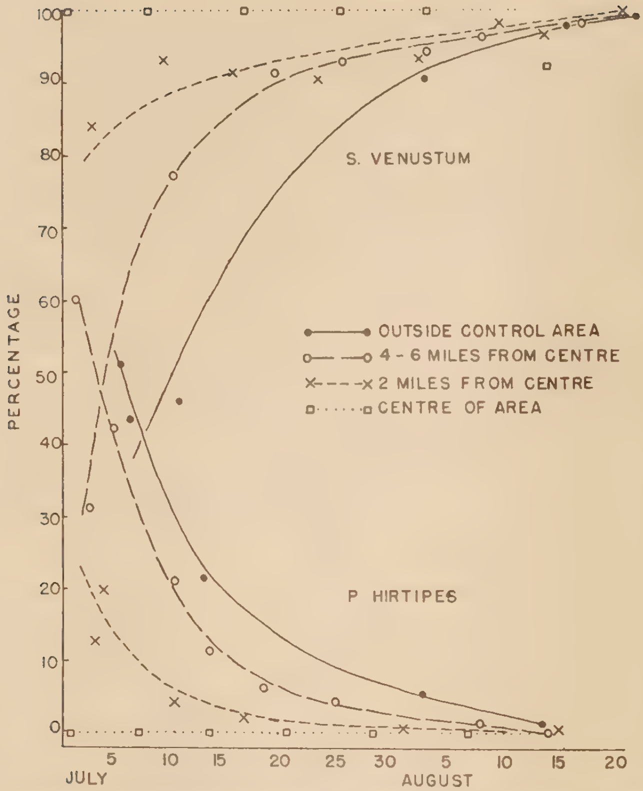

Fig. 4.—Change in percentage composition of the black-fly population plotted against time. Goose Bay, Labrador.

The vector sum of wind velocity during the period of assessment observations gives a mean speed of 2·11 m.p.h. from a bearing of 300°, that is, the over-all movement of air into the area was from a region where there is every reason to believe that there was a very heavy black-fly infestation.

A total of 9,053 specimens were collected in the sweep count material, of which 99·25 per cent. were females of species of blood-sucking flies ; 92·6 per cent. were Simuliids. No males of any species of blood-sucking fly were collected. The black flies, and most of the other biting flies, were identified to species, other material only to family. The relative over-all abundance of the described species of black flies is indicated in the last column in Table I. The numbers of the species insufficiently numerous to be given percentages were : *Cnephia mutata*, three specimens ; *Eusimulium* sp. B, two ; *E. pugetense*, *E. aureum*, an undescribed species of *Eusimulium* and *Simulium vittatum*, one specimen each. The difficulty of separating *P. multidentatum* from *P. hirtipes* is such that a few specimens of the former species may have been overlooked.

The distribution of the more important species other than black flies between the zones is summarised in Table V. The influence of the experimental mosquito control work (Brown & others, 1951) is clear in the first line ; this includes all the black-legged species of *Aëdes*, which cannot be reliably separated when preserved in alcohol. In Table VI, the captures of the more important species are arranged by dates, in 10-day periods. This indicates that the peak population of the black-legged

TABLE V.

Insects taken in sweep samples arranged by zones. Mean numbers captured in 30 sweeps, over the assessment period. Goose Bay, Labrador, 1950.

	Centre	2 mile	4 mile	6 mile	8+ mile	% of total insects taken
Aëdes spp.	0·38	3·2	6·2	5·6	5·8	5·6
A. excrucians (Wlk.) ...	0	0·14	0·2	0·13	0	0·16
A. canadensis (Theo.) ...	0	0·28	0·03	0·06	0	0·12
**Chrysops mitis* O.S.... ...	0	0·03	0	0	0	0·01
C. excitans Wlk.	0	0·07	0·13	0·22	0	0·15
C. carbonaria Wlk.	0	0·17	0·07	0·09	0·25	0·16
Hybomitra metabola (McD.)...	0	0	0·03	0	0	0·01
Culicoides spp.	0	0·14	0·03	0·03	0	0·07
Chironomidae	0·13	0·14	0·1	0·31	0·38	0·23
Braconidae	0	0·07	0·07	0·09	0·12	0·09
Chalcididae	0·25	0·03	0·07	0	0	0·04
Simuliidae	13·6	38·1	50·5	34·8	212·1	92·6

*A new locality record.

Aëdes species was not later than the first week of July. There were 35 specimens not recorded in these tables, distributed among the following groups : Plecoptera ; Hemiptera (Miridae, Anthocoridae, Aphidae and Psyllidae) ; Trichoptera (Limnobiidae) ; Coleoptera (Staphylinidae and Cryptophagidae) ; Hymenoptera (Vespidae and Colletidae) ; and Diptera (Tipulidae, Cecidomyiidae, Mycetophilidae, Bibionidae, Empidae, Phoridae, Tachinidae, Calliphoridae, and Anthomyiidae).

TABLE VI.

Insects other than black flies taken in sweep samples, arranged by 10-day periods. Goose Bay, Labrador, 1950.

	1–10.vii.	11–20.vii.	21–30.vii.	31.vii.–9.viii.	10–19.viii.
Aëdes spp.	175	126	93	77	30
A. excrucians (Wlk.) ...	2	8	1	4	—
A. canadensis (Theo.) ...	1	4	4	2	—
Chrysops excitans Wlk....	10	5	—	1	—
C. carbonaria Wlk. ...	5	4	3	1	—
Chironomidae	7	4	2	10	1
Culicoides spp.	—	1	1	4	—
Chalicididae	1	1	1	2	—
Braconidae	3	—	—	5	1

Discussion.

Valuable as a helicopter is in the application of insecticides to streams and rivers, it does not provide a complete solution to the problem of making these applications in difficult country. A certain amount of rather arduous work on the ground will probably always be required, but routine control would be easier than experimental control. If some suitable type of briquette or disposable dispenser can be developed, which could be either dropped, or, better, lowered into a stream on a thread, the usefulness of the helicopter would be greatly extended.

Figs. 2 and 3 clearly indicate that effective control of black flies at the centre of the area resulted from the extensive application of larvicide to the streams, the effect being very noticeable until at least 5th September. A measure of control was achieved as far out as 6 miles from the centre, manifesting itself in the lack of development of the population peak that normally occurs early in August. Yet it should be mentioned that there were times when black flies were distinctly troublesome between the 2- and 4-mile circles, and even within the 2-mile circle.

The fact that the peaks of attack at the three outer zones in fig. 2 are synchronous strongly suggests that the population in these areas arose by build-up from breeding sites that were overlooked or improperly treated, rather than by infiltration from outside. The greater the distance from the centre, the more difficult it was to be certain that all streams had been discovered. At the centre of the area, however, near which it is reasonably certain that no breeding sites were overlooked, the attack curve reaches its highest point 3 weeks later. This lag probably represents the time required for flies from the other zones to migrate in to the centre. Fig. 3 provides further evidence on this point, in that the average sweep number at the 4-mile circle was higher than that at the 6-mile circle. The site on the 4-mile circle that gave the highest figures was Goose River (4B). This was the nearest site to the only discovered stream that was missed during the treatments, and to the difficult area north of Goose River. If this explanation of the population in the outer zones is correct, more satisfactory control would have been secured if the same amount of effort had been concentrated into work on the 113 square miles within the 6-mile circle, or perhaps into an even smaller area.

Fig. 4 shows clearly the difference in flight habits between *S. venustum* and *P. hirtipes.* At all times the percentage of *P. hirtipes* in the population was less toward the centre of the circle, indicating that this species was moving in toward the centre in much smaller numbers, or much more slowly than *S. venustum*, the percentage of which was always greater as the centre of the circle was approached. This was so in spite of the fact that most of the small number of pupae formed before treatments were probably *P. hirtipes*. It appears that even under the most favourable conditions, with a large population moving into an entirely suitable but completely unpopulated area, it is unusual for *P. hirtipes* to lay its eggs as far as 2 miles away from the place at which it emerged. The situation depicted in fig. 4 represents the combined effect of the relatively slow rate of spread and the fact that there is only a single generation of *P. hirtipes*. *S. venustum,* however, may clearly extend its range by a distance of at least 2 miles during a season, and probably during a single generation, into country from which it has been eliminated. This distance may be as great as 6 miles. There is nothing to suggest that any of the species in this area normally fly the extraordinary distances reported for *S. arcticum*, and suggested for *S. griseicolle* (Edwards, Oldroyd & Smart, 1939).

In areas where *P. hirtipes* is the only important species, the elimination of larvae from all habitats within a distance of 2 miles from a particular locality to be protected should be adequate for at least one season. Where there is much movement of man or animal hosts into a cleared area, however, infiltration is likely to be more rapid. The absence of all species except *S. venustum* and *S. perissum* from collections at the centre of the area suggests that the remaining species are closer to *P. hirtipes* in their flight behaviour than to *S. venustum*. The similarity between *S. perissum* and *S. venustum* may extend to flight habits.

Under certain conditions it might be possible to obtain control of black flies in an area such as that around Goose Bay by the application of DDT from large aircraft on lakes and along important watershed areas ; this would permit considerable economy in man-hours, at the cost of a much larger consumption of insecticide and at the risk of much greater interference with other elements of the fauna. During the whole of this work, no mortality or injury to fish or other economically important animals was brought to the attention of the authors.

Summary.

Twenty-five species of Simuliids are listed with indications of their relative abundance, importance as pests of man, seasonal appearance, temperature requirements, and larval habitats in Labrador. Seven of these are undescribed species. The most important species are *Simulium venustum* Say and *Prosimulium hirtipes* (Fries).

A circular area of 200 square miles around Goose Bay airport was surveyed for important breeding sites. Of 163 streams and rivers investigated, 77 were suitable as larval habitats, and larvae were virtually eliminated from them in June, 1950, by applications of a 10 per cent. solution of DDT in fuel oil at the rate of 1·5 p.p.m.-minutes from a helicopter, conventional aircraft, or boats, or by hand application from the ground. Methods of application are discussed.

The repopulation of the area by black flies was studied, and deductions are made concerning the flight habits of the most important species. On the basis of averages throughout the season, a great reduction in numbers of black flies at the centre of the area was obtained, and a worth-while reduction to a distance of between 4 and 6 miles from the centre. Even near the centre of the area, however, black flies were sometimes troublesome late in the season.

It is suggested that, where *P. hirtipes* is the important species, relief for at least one season could be secured by eliminating larvae within a radius of 2 miles ; for *S. venustum*, 6 miles is suggested as a suitable radius.

No adverse effects on useful animals were recorded.

Acknowledgements.

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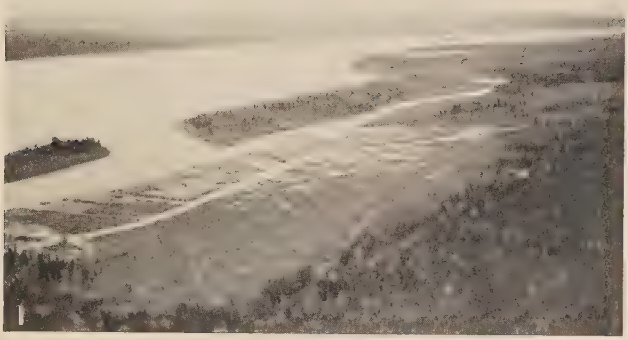
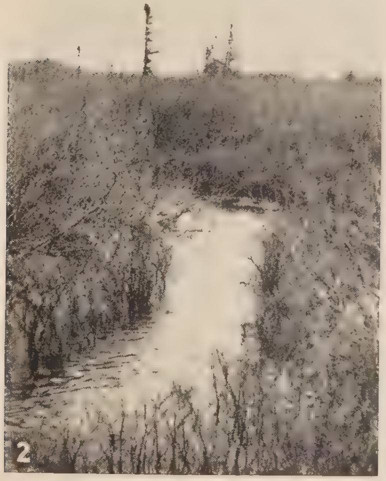




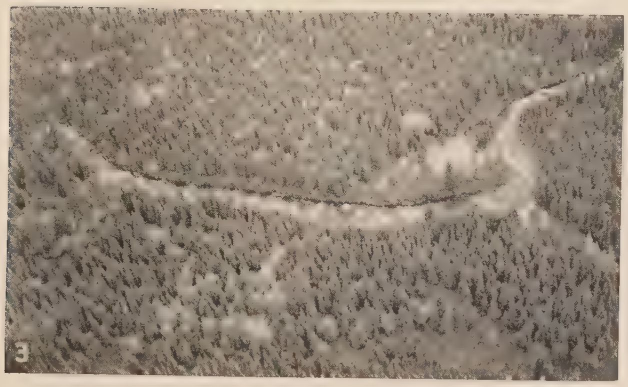
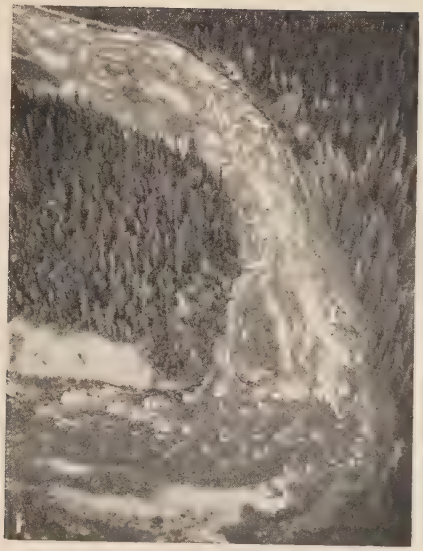


FIG. 1. Hamilton River and Happy Valley settlement, Labrador; Twinn Mountain in right background.

FIG. 2. A large bog stream near Otter Creek, near Goose Bay, Labrador, showing growth of willow and alder.

FIG. 3. A stream in the hills north of the Goose River.



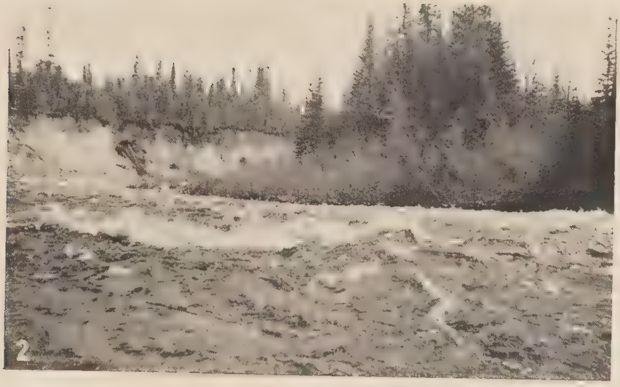


FIG. 1. Helicopter Creek from the air, near Goose Bay, Labrador.
FIG. 2. Rapids near the mouth of Helicopter Creek.
FIG. 3. Helicopter in flight over the Goose River.

CONTROL MEASURES IN 1948–50 AGAINST INSECTS ATTACKING GROUNDNUTS STORED AT KANO, NORTHERN NIGERIA.

By R. W. Howe,[1] L. A. W. Hayward[2] & G. S. Cotterell.[3]

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The original object of the West African Pest Infestation Survey was to investigate, on an experimental scale, the efficiency of a number of control measures in protecting stored groundnuts against the ingress of pest insects. It quickly became apparent in Kano, however, that pest insects especially *Tribolium castaneum* (Hbst.) were so numerous and the damage caused so great that it would be unwise to spend one season on experimental work while leaving the main crop liable to severe damage. Consequently, it was decided that tests of promising methods should be expanded into large scale pilot experiments, which it was hoped could be readily converted to routine. The position was complicated by an outbreak of a new pest, *Trogoderma granarium* Everts, which could only be controlled by fumigation. Nevertheless, a number of other methods were tried, on an experimental scale only, and some practical advice was given on questions of storage methods and hygiene.

Chemical Treatments.

Aqueous Suspensions.

Most of the spraying was carried out with a petrol-driven slow-moving Lister SS2 power sprayer, but some trials of other sprayers were made. The Todd Insecticidal Fog Applicator (TIFA) mentioned below, was also used as a power sprayer using both the wide bore hose and the Eclipse spray attachment. A hand Eclipse sprayer was tried in Kano as well as in Baro where no power sprayer was available. A stirrup pump was also used. Hand sprayers are far too laborious for general use but are suitable where the total area to be treated is small. Eclipse type sprayers enable the spraying to be even and thorough in experienced hands but all African operatives tended to be very superficial in its use. Since it was also a somewhat slow method of application its use was abandoned.

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Application to open air pyramids.

Much of the Kano groundnut storage is in the open air in pyramidal stacks of sacks, so direct spraying of the sacks of nuts, a procedure not previously considered, seemed the only way of protecting the nuts against insects. For this work aqueous suspensions were used, since oil solutions might be absorbed to a greater extent, and there would be taint by the solvent. Also no suitable apparatus was available for large scale oil spraying.

When this spraying of open-air pyramids of groundnuts was first contemplated, it was intended that groups of pyramids should be sprayed on the same day using about four levels of dosage, leaving a control among each group. A plan to perform a series of chemical analyses of sacking and biological tests to estimate the durability of deposits and their effect on the insect population was abandoned, as pyramids had to be covered almost immediately after spraying, and the extra work caused by the *Trogoderma* outbreak coincided with the start of this experiment.

No satisfactory method of estimating insect population accurately was devised and all estimates quoted here are based on opinions made from observations at dusk. It is of interest to note that diminution of population occurred on controls as well as on treated pyramids. This is not unexpected since the adult insects fly at dusk and may then migrate from control to treated pyramids.

Spraying was done with the SS2 sprayer. This was readily transported by kit car in which it was operated as far as possible. Sufficient hose was available for most of the pyramids to be within reach of motorable tracks. Various combinations of swirl plate and nozzle were tried until one was obtained which gave a fine flat spreading jet which would carry a fair distance. This enabled a pyramid to be sprayed by climbing halfway up each side to cover the top, the bottom part being done from the ground.

Much of the spraying was carried out at dusk when the insects were flying ; they were then liable to wetting from the spray as well as subject to the deposit put on the sacking. Wettable powders were weighed out during the day and placed in water but it was found that DDT paste separated out if made long before use. In the dry climate water supplies were frequently cut, so it was found convenient to convey water to the site during the day time. Forty gallons of insecticide proved a suitable quantity to apply to a 750-ton square pyramid on a 50-foot base, ten gallons to a side, but thirty or sixty gallons were usually required for rectangular " cottage " pyramids of 600 or 1,500 tons respectively. Pyramids were usually sprayed in groups of four.

The insecticide generally used was DDT ; BHC was available but was not used much at first because of the risk of taint. Later it was used to a greater extent because DDT was ineffective against *Trogoderma* and because the effect of BHC appeared more persistent and, at the dosages used, it was much cheaper than DDT. In point of fact only one-quarter of the sacks of a pyramid are actually sprayed and it was found that the nett contamination to a pyramid is well within the prescribed limits at the dosage normally used. Mixtures of DDT and BHC were also used. Altogether 15 pyramids were sprayed using 50 per cent. DDT paste ; 27 with 50 per cent. wettable powder ; 64 with 20 per cent. wettable powder ; four with 10 per cent. dusting powder ; 11 with BHC dispersible powder (P520) ; and 24 with mixtures of DDT and BHC. Of the mixtures, one contained DDT paste, 19 contained 50 per cent. wettable powder and four, 20 per cent. wettable powder.

DDT was first used at 100 mg./sq. ft. but this did not seem to be giving adequate results so the dosage was raised and eventually fixed at about 360 mg./sq. ft. All available supplies of wettable powder were used and then, as new supplies had not been received, the dusting powder was used. This dispersed well if kept stirred, and gave an obvious deposit of the diluent dust on the sacks. All the pyramids thus treated had good control, two, very long in storage, being of excellent propaganda value.

New supplies consisted mainly of 50 per cent. powder and paste, since the more concentrated powders were cheaper. Paste was supplied in 12-lb. tins which was the quantity required for an ordinary pyramid and hence appeared most convenient. Unfortunately damage to tins in transit is so great as to preclude their use in practice and the paste was found to deposit as minute lumps on the sacking fibres.

BHC was used at about 12 mg. gamma isomer per sq. ft. but the dosage was increased a little in the hopes of controlling *Trogoderma*. The dosage levels of mixtures were adjusted to give a total dose of the same order as applied as single insecticides.

The treatment of the pyramids in the dry season was a practical success against *Tribolium* which was decreased markedly. There was some increase during the wet season from June onwards, but as a measure of its decrease it was noted that, although during the whole period there were reservoirs of untreated nuts in store in Kano, this insect did not again become the domestic nuisance it was before control was undertaken. Against *Trogoderma* this treatment failed, for some 40 per cent. of all pyramids in Kano actually became moderately infested or worse in spite of a special railing programme designed to remove infested nuts first.

Application to warehouses.

Warehouses were sprayed less completely. In these the spray was applied to the walls, floor and ceiling prior to loading. No direct spraying of produce under cover was proposed since it was feared that the sprayed sacks would not dry and that the bottom sacks would be saturated by the run-off of suspension. However, in one warehouse, in February, 1950, produce badly affected by *Trogoderma*, *Tribolium* and moth (*Ephestia cautella* (Wlk.) and *Plodia interpunctella* (Hb.)) was sprayed without damage. Removal of this stack for fumigation prevented reliable estimation of the success of control.

In general, higher dosages were applied to warehouse structures than to pyramids, because the risk of taint was lower and there was less likelihood of insects remaining on the surface for long periods. The insecticide was applied within a few days of the application of new whitewash, a practice which was encouraged as it ensured the cleaning of premises before spraying. Spraying was, however, found to wash off whitewash from corrugated iron surfaces.

Thirty-eight of the 77 warehouses used for groundnut storage were sprayed, using aqueous suspensions, 32 with DDT, two with BHC, and four with mixtures of these insecticides. The six in which BHC was used contained *Trogoderma* infestation before treatment. Spraying did not control *Trogoderma* infestation but it did restrict its increase. The effect on *Tribolium* was most marked, all untreated warehouses being more heavily affected than those that had been treated.

Application to rick sheets.

One experiment was performed to test the efficacy of spraying the inside surface of rick-sheets just before they were placed on the pyramid. The dose applied was 450 mg./sq. ft. but much of the deposit was removed by handling. There was no visible difference in infestation between this and the adjacent untreated pyramid.

Application to trees and other outdoor harbourages.

In the climatic conditions experienced in Kano, warehouse insects fly actively out of doors at dusk and during darkness. During daylight many of these hide under the loose bark of trees and among vegetation in comparatively cool situations. Any systematic programme of spraying should include treatment of trees adjacent to storage sites and also of the outside walls of warehouses early in the dry season. This was not done by the Survey except for trees very close to pyramids, and the walls of a few warehouses containing large populations of *Trogoderma.*

Oil Solutions.

Application to warehouses.

In general, P31 oil and kerosene were not used as solvents because they were scarce and almost all oil sprays were dissolved in a diesoline oil. The compressors available did not work satisfactorily so oil sprays were not used until the TIFA became available. Then oil sprays were compared with aqueous suspensions against severe *Trogoderma* infestations. The application of high concentrations of BHC in oil proved to be very unpleasant and seemed less successful than water sprays ; the warehouses so treated were not used again for groundnut storage.

The outside walls of all warehouses heavily infested with *Trogoderma* were sprayed with an oil solution containing a mixture of DDT, BHC and pyrethrum.

Application to plinths.

Pyramids are built on special plinths about a foot high. The edge of the plinth is built of ordinary bricks and the foundation of large stones, built up with smaller stones, earth and laterite and topped with cinders. The edge is finished off with concrete or, more usually, with mud, which is surface glazed with a mixture of red clay, cow dung and extract of " dawa dawa " pods (*Parkia filicordea*).

It seemed very unlikely that these plinths which are exposed directly to the hot sun would harbour an insect infestation. As a precaution, however, all plinths were sprayed by the Department of Marketing and Exports with a standard insecticide spray or with plain oil.

Fumigation of Buildings.

Fumigation was not considered a practical control measure when the Survey began work in Kano because few buildings could be made sufficiently gas-tight for good results to be possible. The sudden outbreak of *Trogoderma* in 1949, coupled with the ineffectiveness of other control measures against this insect, left fumigation as the last resource.

Methyl bromide was selected for routine fumigation because its good powers of penetration allow the efficient use of solid stacks, making it possible to utilise all available space in the fumigation buildings. Fumigation could not be done *in situ* because of the unsuitability of the normal warehouses and the absence of light gas-proof material for covering pyramids. Railway wagons could not be used because of the difficulty of sealing them and because of the risk of delaying the turn-round of wagons in Kano. The willingness of the Groundnut Marketing Board to meet the expense of extra transport of the infested nuts made it possible to use for this work some famine reserve stores in Kano which had been built for use as fumigation chambers. Although these buildings were intended to be suitable for fumigation, they have unfortunately the usual ridged corrugated iron roof. There are 17 such buildings arranged on both sides of a rail siding and all are similar in construction.

The walls are of stone set in concrete, rendered with cement on the inside but not treated to prevent the absorption of fumigant. The floors are concrete. Each building is 76 ft. long, but is divided completely into two similar units by a party wall. The internal dimensions of each unit are : length 36 ft., breadth 24½ ft., height at wall 12 ft. and at ridge 19 ft., air volume about 13,700 cu. ft. Each has an entrance in the end, set about 3 ft. above the ground to prevent the entry of rats and so far as possible, units with the entrance close to the sidings were used. They are closed by double wooden-hinged doors which are reinforced by a gas-proof canvas screen mounted on a wooden frame, shutting into a recess lined at the edges with a rubber fillet. The doors lock and the whole was designed to give a gas-proof entrance. Each unit has two small windows about a foot square cemented into each long wall. They do not open and are gas-tight. The roof is made of overlapping sheets of corrugated iron and the ridge covered by a loose-fitting ridge cap. The roof is supported by wooden rafters, with purlins set in concrete.

Twelve of these units were selected for use as fumigation buildings. These were the best available and the Public Works Department made such improvements as were possible to the roofs and the door screens. A hole was made in the top of the wooden door frame and used to pass in the copper gas delivery pipe. The pipe was led across the rafters to discharge in the centre of the store, the end being flattened to give a narrow jet. Simplifex joints were used to connect the 10-ft. lengths of pipe together. Outside, the pipe ran down the wall and was fitted with a specially made adaptor to connect with the gas supply cylinder.

The gas cylinders were placed near the entrances on large scales, each of which was protected from the sun and rain by a rough thatched lean-to shelter. These service cylinders contained about 180 lb. of methyl bromide, and 30 lb. was measured into the fumigation buildings by weight. The gas obtained for routine fumigation contained 2 per cent. chlorpicrin.

The original stock of methyl bromide was flown from Britain by charter plane in service cylinders each weighing approximately 400 lb. when full.

Subsequent stocks arrived regularly by sea in chlorine-type cylinders each weighing about 1½ tons when full and containing 1,800 lb. of gas. They travelled as deck cargo on the mail boats which arrived every three weeks, enabling a fumigation rate of from 300 to 450 tons a day to be maintained in Kano.

These large cylinders, supplied by Messrs. May & Baker Ltd., were scarce, so it was essential that empties should be returned quickly for recharging. Because of the delay caused by a 700-mile rail journey from Lagos to Kano, it was decided to carry out decantation at port. The procedure adopted was to fill the 180-lb. service cylinders from the large supply cylinder and run a shuttle service of the smaller cylinders by rail. Empty service cylinders were sent to Lagos by passenger train and the Railway gave priority railment to Kano for recharged cylinders.

Decantation was performed at Apapa outside a cocoa transit shed, belonging to the Department of Marketing & Exports, which was within reasonable distance of the mail boat berth. The equipment used for decanting was protected from rain by an overhanging roof down one side of the building. The large cylinders were moved from the dockside by lorry, and a mobile crane from a neighbouring railway wagon assembly yard facilitated unloading.

Each 1,800-lb. supply cylinder is fitted at one end with two taps connecting to two internal dip-tubes. The taps are protected by a cap bolted on to the end of the cylinder. During decantation, the cylinder was placed horizontally on the ground with one tap vertically above the other. In this position the upper tap communicates with the free space above the liquid fumigant and the lower supply tap with the fumigant. The cylinder was placed in the sun with the taps under cover.

The 180-lb. service cylinders are fitted with one dip-tube only, the second tap leading direct to the top of the cylinder, each tap being protected by a screw-fitting iron cover. The service cylinders were placed on a 20-cwt. scale and the gas passing over measured by weight ; four empty cylinders could be weighed together and each was charged in turn. The dipstick tap was connected to the supply tap of the supply cylinder by means of flexible but reinforced plastic gas tubing of methyl bromide proof material which was fitted with a tap close to the flange nut fitting the service cylinder. Occasional airlocks were eliminated by slightly releasing the second tap of the service cylinder.

At first no decantation equipment except tubing was available. Whilst waiting for a suitable pressure/vacuum pump, attempts were made to decant by placing the empty service cylinder in a specially constructed ice box, using the sun to heat the supply cylinder. Despite the fact that large quantities of ice and salt were used, it was only possible to lower the temperature sufficiently to half empty the supply cylinder.

On receipt of a compressor/vacuum pump (an Aerograph P5 outfit recommended by Dr Page of the Imperial College of Science and Technology and fitted with a 1½-h.p. engine), the compressor was fitted to the upper tap of the 1,800-lb. supply-cylinder with 16 mm. outside-diameter copper tubing. A pressure of from 75 to 100 lb. per sq. in. was obtained in the supply cylinder with the outlet tap closed. The upper tap was then closed and the outlet taps on the cylinder and on the flexible rubber tubing were opened. The fumigant was weighed as it passed into the service cylinder. When no further change in weight was registered, indicating equalisation of pressure between cylinders, the process was repeated once more by building up the pressure in the supply cylinder. In this way it was possible to recharge a service cylinder in about 30 minutes.

When it was necessary to change from one cylinder to another the tap in the tubing was closed and the flange nut moved, the operator wearing a gas mask and gloves as some liquid methyl bromide escapes during the process. Otherwise little danger was encountered. Care was necessary when releasing the residual pressure before despatching the empty supply cylinder for return shipment.

Once the compressor was available the difficulties encountered were small.

The first supply cylinder arrived with all cast-iron fittings. Exposure to the sea air and to the hot humid coastal climate caused bolts and taps to corrode with consequent difficulty in manipulation. The suppliers promptly remedied this by fitting brass taps and cover bolts, sealing the protective covers.

The gland-nuts of the large and small cylinders varied in size and correct sizes had to be made locally. The Nigerian Railway workshops gave considerable assistance in this task.

The engine of the compressor was always difficult to start. Some difficulty was encountered in efficient servicing, and it is essential that an easy starting, fool-proof engine should be available for African operators unskilled in minor engine adjustments.

Towards the end of the survey, equipment was moved to Kano for decantation there, the Railway promising rapid goods railment of the large cylinders from port to Kano so as to avoid any delay in return shipments of empties for recharging.

Groundnuts infested by *Trogoderma* were first moved to the fumigation site by rail but later 5- and 12-ton lorries were used. Approximately 150 tons of groundnuts could be stacked in each store level to the beams, the triangular roof space forming a useless dead space. Infested empty sacks were thrown on top of the stack. It was difficult to prevent oddities of stacking, particularly the leaving of a well near the entrance.

The gas was weighed in and the store left closed for 24 hours. One day was allowed for airing, and unloading permitted on the third day. Treatment of the whole outside working area with a concentrated aqueous suspension of BHC and spraying of lorries and rail wagons used for infested material was carried out in theory, although it proved difficult to enforce, and on the whole there was little, if any, re-infestation of fumigated produce with *Trogoderma*. Immediate re-infestation with *Tribolium* was usual since those beetles fly actively.

Each day three stores were loaded, three unloaded, three were being aired and three being gassed. This plan was, of course, modified according to convenience and need. It was found, for instance, that the buildings did not hold gas sufficiently well for a day's airing to be necessary.

The routine fumigation commenced on 26th February 1949. By 30th January 1950, over 60,000 tons of infested groundnuts had been treated.

The use of a dangerous fumigant made special precautions necessary, especially as the local population were quite unaware of the dangers and because low concentrations of methyl bromide have insidious long term effects. Two native policemen were put on duty to keep unauthorised persons away from the site, but this precaution failed because the gangs of labourers employed attracted traders. Tests were made on all early fumigations to determine the airing time required and although a halide detector lamp showed little signs of methyl bromide after only four hours airing, a period of 24 hours was at first demanded and a gas mask used when entering the building before this period elapsed.

Fumigant containing a warning agent, chlorpicrin, was used. This warning agent was effective and apparently persisted as long as the methyl bromide. Therefore it seemed safe to hand the task over to the supervision of senior personnel of the local marketing authority.

Gas concentrations and the efficiency of treatment.

The dosage needed in terms of pounds per ton of produce plus pounds per cubic foot of air space were calculated on figures provided by Mr. W. Burns Brown of the Pest Infestation Laboratory, Slough, and rounded off to 25 lb. per warehouse containing 150 tons of groundnuts. Although these figures were applicable to 15°C. and the local temperatures were of the order of 30°C. no reduction of dosage was made because a complete kill was desired, and *Trogoderma* was considered to be resistant and the buildings were expected to leak a little.

The first fumigation was satisfactory but the second was not a complete success because the stacking was very bad. Some sacks fell against the door screen and live *Trogoderma* were found on the screen where the sacks touched. The dose was therefore raised to 30 lb. and the labour supervised strictly to ensure proper stacking. The success of subsequent fumigation was checked by examination for living larvae, and on only one occasion prior to mid-June was a failure indicated by the presence of such larvae.

A number of tests were made to measure gas concentration by the method of Lewis (1945). Generally the lead gas-sampling capillaries were led to gas sampling spears inserted in sacks in the top, middle and bottom layers of sacks in the centre of the building and also to the free air space above the stack.

The first measurement taken on 8th April 1949, gave very low gas concentration so the buildings were immediately checked and repaired once more. After repairs were complete two new tests were made using 32 lb. methyl bromide on 23rd May (fig. 1) and 20 lb. methyl bromide on 1st June. The tests were carried out in the same building and the lower dose used as it was hoped the repairs would enable a more economical dose level to be used. The concentration/time products (c.t.) obtained were 50 and 36 mg./hrs. respectively, much below the figure of 120 which Mr. Burns Brown had found in Britain insufficient to kill *Trogoderma* at 15°C. No live *Trogoderma* were found, however, after these tests.

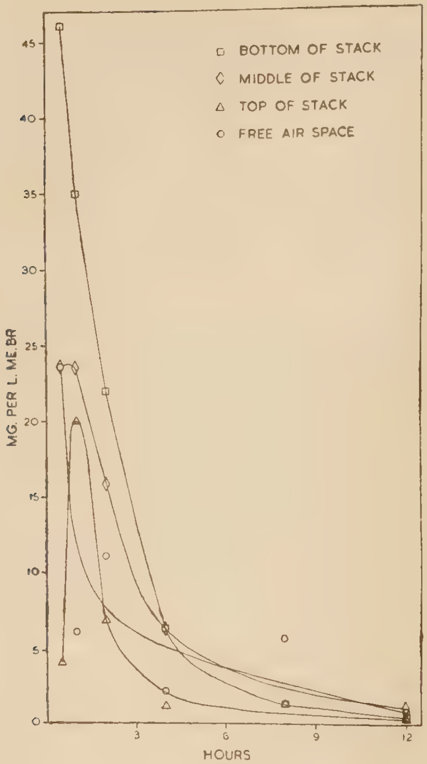

Fig. 1.—Curves showing concentration of methyl bromide in various parts of stack during fumigation using 32 lb. of fumigant, in the fumigation buildings.

No further post-fumigation examination for live insects was made until late August when almost every fumigation showed some signs of failure. The buildings had obviously deteriorated during the wet season.

There was also a gradual easing in the level of *Trogoderma* permitted in nuts exported without treatment. In the opinion of the Survey the level adopted became much too high.

A further examination of the buildings was made in November. By this time, chlorpicrin could be smelt near the doors. The effects of the violent daily and seasonal temperature changes had been to loosen door frames and roof beams, crack the concrete settings of purlins, and make the iron roof sheets gape. Since the site was windswept, there were strong through draughts removing the fumigant. In addition, the doors had warped, rubber fillets were damaged, lost or stolen and nut residues had accumulated round the frames. Some of the gas-proof screens had been damaged and replaced by ordinary porous canvas and others no longer fitted the doors. Gas delivery pipes had been bent by labourers and often sprayed the roof, sometimes near the joints of sheets. Finally stacking had reverted to the unsatisfactory method with a well directing the gas stream to the doorway.

One store was chosen and was resealed using a bitumastic plastic for cracks under the eaves and between roofing sheets and along the roof ridge, painting over it with a tar emulsion. The canvas door screen and the junction of door frame and wall were sprayed with a cocoon plastic and, after loading, the outside of the door was also sprayed with cocoon plastic. Level stacking was achieved. The gas delivery pipe was fitted with an atomising jet. No sampling capillaries were fitted in on this occasion (24th November), but the fumigation was obviously more efficient, since after eight hours of airing there was still a distinct smell of chlorpicrin and the amount of halide present was detectable with a halide lamp.

A fortnight later, sample capillaries were put into this building (8th December) and into a neighbouring one (6th December). On these occasions no special supervision of stacking was made. The second building was not specially treated but was in better condition than most. The specially sealed building was already showing some new leaks, and the door was not sealed externally. Using a dose of 25 lb. of fumigant, the c.t. products for the two were, sealed 67, not sealed 51 mg./hrs. The curve for the unsealed store was very similar to that obtained earlier for the same building, and in shape it suggested rapid leaking. The sealed store never contained as high a gas concentration, presumably because the gas was supplied through an atomiser and not through a pencil jet, but the concentration was maintained better. The c.t. products were still not adequate and it seems certain that these buildings can never be satisfactorily treated without drastic modification, the most important needs being a flat concrete roof and more suitable doors.

Fumigation of Pyramids.

Transport of groundnuts to fumigation buildings for treatment was a laborious and costly operation which caused an extra double handling of the nuts, and tended to spread infestation over the whole storage area. For this reason the feasibility of fumigating pyramids *in situ* was investigated.

Although it was known that the rick-sheets were not gas-tight, a test was made of the efficiency of fumigation of a pyramid *in situ* under these sheets. Two small experimental cottage-shaped pyramids, each about 33 × 18 × 16 feet vertical height, 4,800 cu. ft. volume and about 150 tons capacity, were constructed with a copper pipe built into each, ending internally in the middle of the pyramid some eight feet from the ground and externally adapted for connection to a gas cylinder. The two pyramids were covered by rick-sheets in the normal way and each eventually developed a severe infestation of *Trogoderma.*

On two occasions (1st June and 3rd September, 1949) the two pyramids were gassed, one with 20 lb. and the other with 40 lb. of methyl bromide on each occasion. The halide detector showed a considerable escape of gas especially at the base on the lee side of each pyramid, and it was evident that no practical control had been achieved. One pyramid was dismantled in November and was shown to be infested throughout. The other was retained for a further experiment using five two-ply rubber dinghy sheets sufficient to cover the experimental pyramid and a cocoon plastic for building a seal over the joins between the sheets, together with the accessories for applying it, namely, an adhesive, a webbing agent, a paint spraying gun and a compressor. Before the pyramid was sheeted, the ordinary rick-sheets were removed and three layers of sacks removed to give a flat top. A few sacks were left along the long edges and a pole was placed along each, so as to support the sheets over a well of free space. Methyl bromide was to be introduced into this free space through four atomising jets, spaced equidistant along a copper pipe running the length of the pyramid and the liquid was to be led from a cylinder by a copper pipe passing through the sheeting to the top of the pyramid and to be blown into the pyramid by compressed air. The gas delivery tube, and lead sampling capillaries, which passed through the sheeting, were sealed to it with the cocoon plastic. The lead capillaries for taking gas samples were inserted at six points, inside sacks at the top and bottom of the west end, inside sacks at the top and half-way up on the north side, in the free space at the top and also along the built-in copper tube to the centre of the pyramid.

After the sheets had been fixed and all holes sealed, the sheets were held tightly against the side of the plinth by rolled-up rick-sheets and heavy stones.

Thirty pounds of methyl bromide were applied. Only very slight traces of escaped gas were detected by a halide detector. Gas samples were taken using evacuated flasks containing monoethanolamine, at ½, 1, 2, 6 and 16 hours after dosing was completed. These were analysed by the method described by Lewis (1945), slightly modified.

The sheets were removed 2½ days later and at that time the odour of the warning agent chloropicrin was readily noticeable. No living insects were found. The c.t. curves obtained are shown in fig. 2 and it will be seen that the concentrations obtained were considerably above those obtained in the normal fumigation buildings and were held considerably better. Therefore it was considered worth while to treat a commercial pyramid.

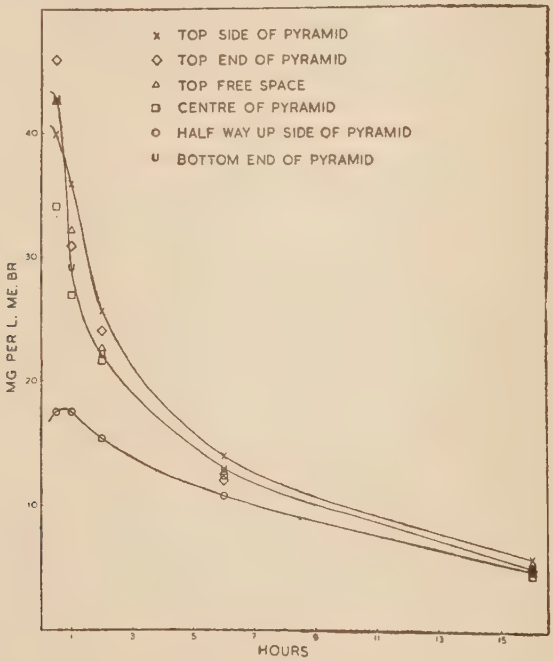

Fig. 2.—Curves showing concentration of methyl bromide in various parts of experimental pyramid fumigated under sealed sheets using 30 lb. of fumigant.

A commercial pyramid heavily infested by *Trogoderma* was selected for treatment. Its dimensions were : base, 50 ft. square ; height of side, 7 ft. vertical plus 37 ft. sloping ; volume, approximately 29,000 cu. ft. ; tonnage, prepared for fumigation, 742. The top four layers of sacks were removed and also a few from the centre of the next layer to form a well or expansion chamber. Four atomising jets were arranged as an H in the well and connected as before, by a copper pipe down one side of the pyramid to the gas cylinder. Lead gas-sampling capillaries were inserted at five points, inside bags at the top, middle and bottom of the west side of the pyramid and in free space at the top and bottom.

The five dinghy sheets were separated by cutting the old seals and, together with three large sheets of balloon fabric, were placed on the pyramid, fixed and sealed together as before. All holes in the balloon fabric were repaired with cocoon plastic. The sheets were held against the pyramid plinth by a continuous row of sacks of clean new-crop groundnuts. A full cylinder of methyl bromide, 179 lb. was emptied into the pyramid, pressure being maintained by means of a compressor.

The sheets were left in place for a week and the pyramid was left standing another month. No live *Trogoderma* were found in the pyramid in this period or anywhere in it during dismantling.

Comparison of Pyramid and Warehouse Fumigation.

Complete mortality appeared to have been achieved in both pyramid fumigations. The minimum c.t. products obtained were much above those obtained in the fumigation buildings (162 and 174 as compared with 67) in which a number of surviving *Trogoderma* larvae were often found. A factor contributing to the lower c.t. product in these buildings is the relatively large dead air space above the beams, for 150 tons of nuts are occupied in a volume of 13,700 cu. ft. as compared with a volume of 4,800 cu. ft. under the sheeting. A second factor is the difficulty of keeping buildings that respond to climatic changes adequately sealed, whereas the sheets could be satisfactorily sealed. It is interesting to note that the loss of gas through or to the plinth was not important.

Circulation of gas was helped by the flapping of the sheets which at times was quite violent, especially for the small pyramid. Convection currents were also likely with internal temperatures in the region of 40°C. and external temperatures changing sharply at dusk and dawn. The small pyramid was gassed about one hour, and the large about six hours before sunset.

Since gas was liberated over the centre of the pyramid, it could be expected to fall slowly through the middle, spreading slowly outwards, with some rapidly spilling down the outside under the sheets and collecting at the bottom. Consequently minimum concentrations would be expected half-way up the outside of the pyramid. In these pyramids, adequate c.t. products were detected at these points. Fumigation of small commercial pyramids therefore seems practicable, but a large 2,000-ton cottage-shaped pyramid now needs to be treated to complete the picture.

One sampling line in the large pyramid gave a very low concentration curve throughout and was assumed to be faulty because a high kill was obtained at the point sampled.

Removal of the sheets from the pyramid without damage was simple, but the balloon fabric made the complete tent too heavy to carry. As a result it was a little damaged in moving it some fifty yards to another infested pyramid and further damage was done fitting it on to this pyramid. These very heavy sheets were managed sufficiently well for it to be probable that prefabricated tents made entirely of light dinghy sheets would be easily moved from one pyramid to another without damage.

Fumigation with Ethylene Dichloride—Carbon Tetrachloride Mixture.

Some of the famine reserve stores contained small quantities of guinea corn used for food in the local boarding schools and prisons. The infestation of this corn periodically increases sufficiently to make fumigation necessary, a task normally carried out by the Agricultural Department, but taken over for a short period by the Survey. The standard fumigant used was a mixture of ethylene dichloride and carbon tetrachloride (3 : 1) and this was applied as a liquid poured on to the sacks of corn from a watering can. Although this fumigant does not penetrate well, no special restacking was needed as each of the two stores treated by the Survey in December 1948 contained only between 50 and 100 tons each, all loosely stacked.

Each store had a capacity of 13,700 cu. ft. and 33 gallons of fumigant mixture were used. The stores were left closed for six weeks and on opening it appeared that the fumigations had been entirely successful.

The insects present in the grain of both stores were the usual corn infestations of *Calandra oryzae* (L.), *Rhizopertha dominica* (F.), *Tribolium castaneum* (Hbst.) and *Sitotroga cerealella* (Ol.). The major reason for this fumigation, however, was the presence in one of *Trogoderma granarium* Everts, recorded as a stored grain pest for the first time from Nigeria.

By June, *Trogoderma* had become established at Baro, a port on the river Niger some 400 miles from Kano. At the time the river was not navigable, so that continued storage of the infested groundnuts was inevitable. There were no premises or barges available suitable for fumigation and an attempt was made to use the ethylene dichloride-carbon tetrachloride mixture without interfering with the solid stacking of the sacks. Spaces under the eaves and under doors were stuffed with sacking. The two stores contained 324 and 890 tons respectively and each was treated with 132 gallons of fumigant.

The external infestation was controlled but a considerable population of *Trogoderma* survived inside the stacks and later multiplied.

Todd Insecticidal Fog Applicator (TIFA).

In warehouses.

Early in 1949, soon after the outbreak of *Trogoderma* was discovered, a Tifa machine was tested in collaboration with Mr. Freshney. The production of fogs or mists which could be blown into warehouses was worth a trial for most of the infested warehouses in Kano were so fully loaded that it was impossible to gain access to apply other treatments. As far as possible, therefore, the leaks in infested stores were closed with sacks and fogs or mists were blown into the most badly affected stores. Much fog escaped but it was evident that insecticide was forced into some of the inaccessible crannies. Deposit tests on glass plates showed that the insecticidal deposits were small at places in the warehouses remote from the points of application, but observation soon after treatment suggested that this treatment had had some inhibitory effect.

Later, monthly applications of small concentrations of insecticide were tried in about twenty warehouses. Three stores were treated in a day with eight gallons of a standard diesoline oil insecticide containing 5 per cent. DDT (4 lb. technical) and 0·35 per cent. BHC (24 oz. LG140) together with a little pyrethrin concentrate. This routine was performed by the Department of Marketing and Exports for several months using particle size 24. This treatment gave some protection against *Trogoderma* up to October when the fogging ceased. No protection against *Tribolium* was noted.

In June 1949, trials were made with the TIFA applying the phosphorus insecticides, hexaethyltetraphospate (HETP) and tetraethylpyrophosphate (TEPP). Each insecticide was applied as a fog in diesoline oil and as a spray in water to warehouses containing heavy infestations of *Trogoderma*. In addition, test specimens of *Trogoderma* and *Tribolium* larvae and adults were placed in beakers at points close to and very remote from the point of application.

It was found that these rather dangerous insecticides could be applied safely using the TIFA but that the insecticides were not very promising against either *Trogoderma* or *Tribolium* ; the test larvae used for TEPP were still active after three days but those used with HETP were moribund. Four pints of HETP (16 per cent. active principle) were used in a gallon of oil or water and applied in 3 minutes and 1·6 pints of TEPP (40 per cent. active principle) in 1¼ gallons of oil or water were applied in 3¼ minutes. TEPP had no effect at points remote from the applicator but HETP killed or drove insects into hiding at fairly distant points. Insects reappeared, however, within three days.

In covered pyramids.

After rick-sheets had been placed on pyramids, a number of the pyramids were fogged using the standard BHC-DDT-pyrethrum mixture. The fog was directed under the sheets through a special pipe, each accessible corner of the pyramid being used in turn. Much fog escaped between and under the sheets and even through the pores of the poorer sheets. It was evident from the points of escape that the fog penetrated between the sheets over the entire surface of the pyramid but little control appeared to be achieved.

One small pyramid was specially constructed with a pipe built in for the insertion of a fog. The pipe was three inches in diameter and 1-in. holes were bored in it at 6-in. intervals. Vertical and horizontal sections were joined with a right-angle iron bend and the rick-sheets draped round the projecting part of the horizontal length. Two gallons of standard insecticide were applied as fog on two occasions, 4th June and 2nd August, using particle size 24. The fog escaped fairly uniformly indicating a reasonable distribution inside. This treatment afforded some control of *Trogoderma*, since this insect became numerous early in the neighbouring pyramid built of nuts from the same source, but only slightly affected the treated pyramid.

For open air fogging.

It was thought that it might be useful to allow fog to drift over pyramid sites, so this was tried on an unsprayed site at dusk. *Tribolium* and *Ephestia* were flying actively and a dense fog of standard insecticide was put round the whole site giving a complete coverage which did not drift away quickly. The flying insects appeared unaffected for the beetles and moths caught flying survived as long as controls.

Two pyramids were fogged with standard insecticides immediately after spraying with BHC whilst they were still wet, resulting in obvious deposits of oil on the wet sack hairs. Control of *Tribolium* was clearly better on these pyramids than on their neighbours and they were the only ones on this site to remain free of *Trogoderma*.

Smoke Generators.

The use of smoke generators on a large scale was not envisaged on account of the nature of the buildings. They were used sporadically when suitable, usually at a much larger dose than recommended to overcome the loss through holes in the buildings. Three examples of their use are mentioned.

A small quantity (about 50 tons) of guinea corn stored in a fairly air-tight building, capacity 13,700 cu. ft., became heavily infested by *Sitotroga*, *Calandra oryzae* and *Tribolium castaneum*. Two fumite (DDT) generators each suitable for 10,000 cu. ft. were used. A few days later it was seen that control was good, but not complete as some *Tribolium* were still active. Two months later *Trogoderma* was found in this warehouse which had not been disturbed in the interim.

Four closed railway wagons each of 1,800 cu. ft. capacity were loaded in error with 20 tons each of groundnuts heavily infested with *Trogoderma*. No sealing of wagons was attempted. Two No. 2 Gammexane (BHC) smoke generators were used in each wagon, leakage through the ventilators and door cracks being very obvious. Wagons were examined quickly four hours later when there was an obvious deposit of BHC powder. There was no apparent insect control.

Three adjacent warehouses with air spaces connecting near the roof and known to be heavily infested with *Trogoderma* were loaded with groundnuts very heavily infested by *Ephestia cautella* and *Tribolium*. The three buildings with a capacity of approximately 120,000 cu. ft. contained about 2,000 tons of nuts. Three DDT generators each suitable for 10,000 cu. ft. and twelve No. 4 Gammexane generators were used. *Trogoderma* and *Tribolium* appeared unaffected but the large adult *Ephestia* population was killed. New adults appeared in a few days, however.

Admixed Dusts.

Three imported insecticidal dusts and one imported inert dust were available for practical trial at the start of the 1948–9 groundnut season. The dusts were admixed with nuts at the storage sites. Each treatment was administered to units of five sacks, each unit being replicated at least three times. The admixture was made on a rick-sheet placed on the ground, the required amount of insecticidal dust being mixed with the contents of three sacks at a time. The nuts were rebagged, samples taken for moisture measurement, the sacks were then weighed and loaded into commercial stacks, as far as possible the sacks of a unit being adjacent. When the stack was unloaded in the normal course of events, the experimental sacks were re-weighed, the dust sieved off and weighed and a moisture sample determined. The loss of weight, adjusted for moisture change, weight of groundnut dust, and added insecticidal dust was taken as a measure of damage by insects and hence of the degree of control attained. No measurement of insect numbers or mortality was attempted.

Pyrethrum flowers.

Powdered pyrethrum flowers were obtained from Kenya in two batches. A small quantity was sent by air arriving early in the season. This was used at a low dosage level in three pyramids. A larger quantity sent by sea arrived late in the season and was used in large doses in two warehouses.

The rate of application used in the pyramids was about ¼ per cent., *i.e.*, ½ lb. per 189 lb. sack of groundnuts. These experiments were spoiled by water damage but indicate some real protection in outside bags where damage was reduced by half (Table I).

TABLE I.

Total weight loss in oz. per 189 lb. bag of groundnuts stored in pyramids for 11–12 months, treated with powdered pyrethrum flowers admixed at rate of ¼ per cent. (weight loss adjusted for moisture change and including weight of insect frass in bags).

Position in stack	Weight loss in oz.		Remarks
	Control	Treated	
Outside	211	108	No *Trogoderma*
Outside bottom ...	198	138	Slight *Trogoderma*
Near outside... ...	58	55	No *Trogoderma*
Near outside bottom	77	50	Slight *Trogoderma*
Outside	120	68	Much *Trogoderma*
Intermediate ...	—	49	Much *Trogoderma*
Inside	53	32	Much *Trogoderma*

Control and treated pairs each in the same pyramid.

Dosage rates up to 1½ per cent. were used in two warehouses where some gains in weight were observed among the treated sacks, indicating a possibility that the dust is hygroscopic. In one warehouse there was no observable change of moisture content during the experiment. In the other in which 16 sacks at each dose level were placed systematically through an experimental stack of eight sacks each way, the moisture change was confused, but as it appeared to affect all treatments equally, the treatment levels may be safely compared. The pyrethrum powder certainly exerted some control in these experiments and a dose level of 1 per cent. is indicated as useful (Table II).

TABLE II.

Total weight loss in oz. per 189 lb. bag of groundnuts stored in warehouses with powdered pyrethrum flowers admixed at various dosages. (Weight loss adjusted as in Table I.)

Dose of pyrethrum	Weight loss in oz.	
	Warehouse 1	Warehouse 2
	Stored for 6 months	Stored for 10 months
Nil	78	—
½ lb.	—	150
1 lb.	64	83
1½ lb.	—	92
2 lb.	47	68
2½ lb.	—	73
3 lb.	53	40

BHC, DDT and silica.

These dusts were used in two pyramids and one warehouse. DDT was used at the rate of 100 p.p.m., and assuming the commercial sample to be pure, this is much above the level permitted in Britain. To each sack 8·5 gm. of dust were added and to make mixing possible, the insecticide was first diluted with ½ lb. of insect frass. BHC was similarly used at a level of 13 gm. of DO34 per sack, diluted with frass before mixing ; this is at a rate of 6 p.p.m. of total isomers, about 50 per cent. above the level then allowed in Britain. The inert silica dust was used at the rate of one pound to two sacks in pyramids and one pound to three sacks in the warehouse.

Table III summarises the results obtained from one pyramid, the only satisfactory experiment performed. The treated bags in the other pyramid were placed in the bottom layer and were all to some extent spoiled by water damage or by termites eating the sacking. The scanty results obtained showed some reduction in damage compared with controls.

TABLE III.

Total weight loss in oz. per 189 lb. bag of groundnuts stored in a pyramid for 11 months with various insecticidal dusts admixed. (Weight loss adjusted as in Table I.)

Treatment	Weight loss in oz.	
	Outside bags	Inside bags
Control	211	58
BHC 6 p.p.m. ...	113	56
DDT 100 p.p.m. ...	97	44
Pyrethrum ¼% ...	108	55
Silica ¼%	88	52

The warehouse experiment was also spoiled, but since on this occasion the spoilage was due to a heavy infestation of *Trogoderma* present at the time of loading, the dusts can be reckoned to give little protection against this insect. The attack of *Trogoderma* weakened the sacks which needed extra special care on removal from the stack to avoid breaking them. The results obtained shown in Table IV indicate that little reduction in damage can have been caused for losses vary between 3·5 and 9·5 per cent.

Further laboratory experiments with dusts.

Although these exploratory field tests were performed, it was not thought that admixed dusts offered any practical promise. Admixture offers practical problems which though not insurmountable are discouraging ; if carried out at storage centres there is a considerable amount of extra rebagging involved and if at buying centres then transport of the dust to these centres is costly. The use of a compressed air gun for injecting the dusts into outer sacks only is a suggestion which is promising but when the Survey ended, only the early stages of practical trial were reached owing to the absence of a suitable compressor. Further, the regulations place a limit on the amount of " sand " present in nuts and to add dusts deliberately would be to encourage the addition of other foreign matter.

TABLE IV.

Total weight loss in oz. per 189 lb. bag of groundnuts stored in warehouse for 9 months in presence of very heavy *Trogoderma* infestation. Methods of protection used include admixed dusts and impregnated sacks. (Weight loss adjusted as in Table I.)

Treatment	Position in stacks			
	Outside top	Outside bottom	Inside top	Inside bottom
BHC	234	166	d	117
DDT	d	154	174	124
Silica	285	231	157	110
DDT impregnated sacks	d	d	144	d

d—sacks burst by *Trogoderma* damage.
30 oz. is equivalent to approximately 1 per cent. loss.

Therefore no further work on admixed dusts was envisaged until a suggestion was made that a "handful of any dust" placed in a sack of nuts would contribute to the control of *Trogoderma*. Some Nigerian rocks were obtained and ground in a pestle and mortar, but not micronised. These were used in laboratory tests against *Trogoderma* larvae. Commercial inert silica was added as a control and a test was also made of a BHC dust used in Kenya, Kensil G.025. The dusts were spread in thin layers in petri dishes at 30 and 70 per cent. relative humidity and mortality recorded every day.

The dusts which gave the best results in these experiments were used again in further experiments in which nuts were shaken up with the dusts so that they became coated with dust before being subjected to the attack of *Trogoderma* larvae. Table V gives the best of the results ; only a diatomite from Bornu gave any encouragement, being better than silica in Experiment No. 4 in the presence of food. The BHC dust gave surprisingly poor results.

TABLE V.

Mortality percentage of *Trogoderma* larvae exposed in groups of 50 to various insecticide dusts in petri dishes at two relative humidities at about 30°C.

Dust	Spread in thin layer with no food				On nuts with adhering dust		On nuts on thin layer of dust	
	Expt. 1		Expt. 2		Expt. 3		Expt. 4	
	6 days		10 days		28 days		28 days	
R.H.	70%	30%	70%	30%	70%	30%	70%	30%
Silica	76	82	—	—	26	38	44	60
Kensil G025 ...	58	52	32	22	24	58	—	—
Diatomite (Bornu)	36	36	28	48	24	24	70	76
Volcanic Clay ...	44	44	62	26	12	24	—	—
Volcanic Tuff ...	30	46	58	14	16	16		
Control	—	—	16	14	18	10	18	10

The local diatomite might give very good results if micronised in a ball mill, but the transport charges might be high. No other local dusts merit consideration except the volcanic products. These tested included granites, clays, calcrete, coal, lignite, limestone and clinker.

Dusts spread in Warehouses and in the Open.

An attempt to spread a BHC dust on the surface of a pyramid confirmed that even a slight breeze carried the dust away. However DO34 was successfully applied to the cinder surface of a pyramid plinth at a dose of 0·4 gm. /sq. ft. using a power blower. No *Trogoderma* carried over from the plinth to the new pyramid but it is doubtful if the insects could withstand the hot sun which shone all day on the plinth.

Dust barriers at the base of walls were not tried since it was not usual for space between stack and wall to be available. In two warehouses pyrethrum flowers were spread at a rate of one ounce per sq. ft. on the entire top layer and also on the two outer rows of sacks in every layer. There was no indication that this treatment was effective. One warehouse contained a large *Tribolium* population and the total weight loss (including frass) per sack weighed was about 8½ lb. The other contained *Trogoderma* when loaded and, in addition, had been sprayed with aqueous BHC. Treatment appeared successful up to unloading when it was found that the infestation was very heavy though not very apparent externally. The average total weight loss per sack was about 9¾ lb.

Sacks impregnated with DDT.

A number of jute sacks impregnated with DDT in Britain in September 1947 were incorporated into a pyramid in December 1948, and into a warehouse stack in April 1949. The latter was known to be infested by *Trogoderma* and the former was eventually also infested. In both cases the impregnated sacks suffered severely from *Trogoderma* damage and obviously afforded no protection. In the warehouse (Table IV) only 12 of the 40 sacks used were recovered intact, and the damage to nuts was heavy. In the pyramid one whole set of five bags was lost. In the remaining outside bags there was an average loss of 5 lb. 6 oz. per sack, an improvement of nearly 30 per cent. over the controls (7 lb. 8 oz.) but for inside sacks the average loss per sack, 3 lb. 4 oz., was the same as the control.

The theoretical levels of proofing were 0·5, 1·0, 2·5 and 5·0 per cent. In June 1948 the actual range was 2·7 to 5·2 and this had fallen to 1·6 to 4 per cent. by

November. It is possible that these levels had fallen considerably more by the end of storage.

OTHER TREATMENTS.

Traps.

Traps such as are used in southern Nigeria were not tried as a control measure although plates of liquid were used to determine the species present. The large surface of liquid needed to catch a significant number of insects rules out this as a control method. The nightly movement of insects to the open for the dusk flight would make it well worth while testing various sticky compounds on screens placed over doorways, windows, and ventilators, to determine the life of the sticky compounds in dry dusty conditions.

Heat Treatments.

The use of driers was considered and abandoned in face of the fuel problem with a crop of 300,000 tons requiring treatment. All fuels whether wood, coal, oil, or electricity are either scarce or expensive.

Driers would combine the functions of drying further the nuts which are already dry and of killing the insect population in the nuts. Adult insects except *Trogoderma* would escape because the disturbance would stimulate flight, and the heat-treated nuts would quickly be re-infested under present conditions. It is possible that further drying of the nuts would reduce the moisture content so much that *Tribolium* could not maintain itself on them until the rains commenced but this is unlikely.

DISCUSSION.

The best Use of the Insecticides tested.

The above work was qualitative and unscientific except for that on dusts, in which weight loss was adopted as the criterion of efficiency. Nevertheless some definite impressions have been gained in the course of the practical work performed.

DDT appears to be less effective than BHC against *Trogoderma* and *Tribolium* and also is more expensive at the levels used. Consequently BHC as a wettable powder appears to be the most promising spray for future use in warehouses and on pyramids.

To incorporate pyrethrum some oil sprays were used. On the basis of one test, it appears to be possible to add pyrethrum in P31 with a little soap, to a water suspension of BHC or DDT and to get good emulsification. If this type of suspension proves satisfactory, solutions of these insecticides and pyrethrum in oil need only be used as fogs applied to pyramids still wet from spraying. Mists of insecticides in water suspension could replace fogs in routine treatment of infested warehouses with a consequent reduction of costs and elimination of the risks of oil taint to produce.

Pyrethrum as a powder appears to be effective admixed in outside sacks.

The Problem of Storage Hygiene and Practice.

Once insects are admitted to be important in storage conditions, and control work undertaken, storage hygiene should be improved to avoid practices liable to nullify the control measures. In addition, administration should ensure that as far as possible all regulations are designed to aid control.

In the primitive conditions of storage in Kano it was possible for the Survey to suggest several improvements which were practical and to find many undesirable practices that are unlikely to cease.

A very undesirable feature of stacking in Kano warehouses was to fill every available space leaving no inspection gangways, and, in fact, making no inspection during storage. This has now improved, for some regular inspections are made and stacks are not placed hard up against warehouse walls. Sufficiently wide inspection gangways are still rare and unsteady stacks often make them unsafe.

The main purpose of storage hygiene is the prevention of the unnecessary spread of insects. Before the appearance of *Trogoderma*, therefore, the absence of store hygiene unless universally practised was not very important because the other pests spread readily by flight. Under the conditions now prevailing, hygiene should be directed to prevent the spread of *Trogoderma* within a crop and of all species from the crop of one season to that of another. The latter is best done by segregating the crops, either in time, by exporting one some months before the other arrives, or in space, by storing the two crops some miles apart. The destruction of all infested crop residues and the fumigation of tools such as sacks, rick-sheets, etc., should serve both objects.

The *Trogoderma* problem demands the use of common sense on the part of all handling groundnuts, and rigorous dis-infestation of infested tools and areas. This requires that Produce Examiners be thoroughly conversant with the dangers, have the powers to deal with incidents and probably be reinforced in numbers to meet the extra duties involved. Such processes as winnowing infested nuts in the open air in the wind must be replaced by methods of sieving off dust and insects into a box such as the Survey used, and burning of the waste. Before leaving infested sites all workers should clean their clothes, especially shoes, trouser turn-ups and hats, but these will always spread some insects.

Much improvement in the hygiene of work on the storage site is unlikely and the most helpful method of improvement seems to be by administrative changes. For instance, the handing back of the responsibility of allocating railments to the Department of Marketing and Exports is a necessary step so that railments can be planned according to insect infestation. This certainly reduced the *Trogoderma* problem in 1949. The usual mistake then was to overlook the spread of *Trogoderma* by handling heavily infested lots in the vicinity of clean lots. Rational planning would move clean lots first to give enough space to handle the infested stock but it was not easy to decide on the best use of the limited number of railway wagons available.

Another administrative change is needed to prevent the presence of *Trogoderma* being an advantage to agents holding nuts. The priority given to railing infested stock gives the agent an earlier return of his capital and frees his storage space for other produce. Consequently there is some encouragement for an agent to have infested nuts, especially as he does not have to bear the losses caused by the insect. There is thus some justification for a simple price differential between nuts with heavy, light, or no *Trogoderma* infestations, coupled with a rising price to the agent, as the period for which he is compelled to store increases.

A simple price differential between infested and clean stock might also get to the root of the *Trogoderma* trouble, since this seems to be largely caused by storage of nuts by middlemen for a year before sale to agents. It seems pointless to declare this practice illegal as it is not easy to detect and, in any event, is a reasonable action if done without impairing the quality of nuts. If the price depends upon quality many unsatisfactory features of the present trading methods will gradually be eliminated without difficult legal problems or the introduction of regulations which cannot be enforced.

Summary.

The control methods used to protect new-crop groundnuts stored in Kano against insect attack are described.

The main method used was the spraying of aqueous suspensions of DDT directly on to the sacking of piles stored in the open and on the walls of warehouses before the nuts were stacked. The solutions were applied with a slow-moving orchard power sprayer, and 50 per cent. wettable powder applied at the rate of 360 mg. /sq. ft. was found satisfactory. The BHC wettable powder applied at about 12 mg. /sq. ft. was cheaper and equally as good and has now been found safe. Treatment markedly reduced the *Tribolium* population but had little effect on *Trogoderma*. Sprays of oil solutions were little used and were not very satisfactory.

To combat *Trogoderma*, fumigation with methyl bromide in the best buildings available in Kano was tried but it was found that the gas was not satisfactorily retained. This made the process much safer in that the airing period needed was reduced but even with a high dose of methyl bromide (30 lb. per 150 tons) a concentration time product only of the order of 50 mg. /hrs. was obtained. This appeared to be just sufficient to give a complete kill of *Trogoderma* larvae at Kano temperatures (just over 30°C.).

The severe climate caused the buildings to deteriorate rapidly but repairing the worst defects immediately gave a marked but temporary improvement. It is impracticable to obtain really satisfactory results at Kano in buildings with ridged iron roofs and it is suggested that flat concrete roofs and more suitable doors be fitted to the fumigation buildings.

Fumigation of pyramids *in situ* under ordinary rick-sheets was a failure as the sheets were not gas-tight, but successful results were obtained when the pyramids were covered with gas-tight rubber sheets sealed together with a cocoon plastic. Complete kill of a large population of *Trogoderma* was apparently achieved in both a 150 ton experimental pyramid dosed with 30 lb. of methyl bromide and a 750 ton commercial pyramid dosed with 179 lb. Much higher c.t. products were obtained than in the permanent fumigation buildings, presumably because of the much smaller air space under sheeting and the small loss through leaks. Evidently loss through the cinder base to the earth is not important and weighting the bottom of the sheets against the pyramid plinth by sacks of groundnuts or rolls of rick-sheets was efficient. Flapping of the rubber sheets and sharp surface temperature changes caused good circulation of gas and gas distribution was quite even. Lowest c.t. products were obtained half-way up the pyramids.

The fumigation of groundnut pyramids *in situ* under prefabricated tents appears to be a practical proposition.

A mixture of ethylene dichloride (3 parts) and carbon tetrachloride (1 part) at the rate of 33 gallons to just under 100 tons of guinea corn, loosely stacked in a building of capacity 13,700 cu. ft., gave successful control of the insect pests present including *Trogoderma* and *Tribolium*. The same fumigant was useless against these insects in closely stacked groundnuts.

A Todd Insecticidal Fog Applicator was used to introduce fogs into warehouses loaded too full to permit entry of operators or equipment Regular treatment with a standard insecticide appeared to check *Trogoderma* slightly but had no effect on *Tribolium*. Results with the phosphorus insecticides HETP and TEPP which were used as fogs and water sprays were not good, but HETP was better than TEPP. The application of fogs under the rick-sheets of covered pyramids gave little control but introduction to the centre through a built-in pipe gave encouraging results. Allowing a fog to drift over pyramids appeared useless but there was a marked deposit on a pyramid still wet from previous spraying. Smoke generators were useful in limited circumstances.

The use of admixed dusts appears impractical, and in any event should be restricted to outer sacks. Silica, pyrethrum and BHC at reasonable dosages, and DDT at an exceptionally high dose, all reduced damage by half in the outside sacks of the pyramids. In the presence of a heavy *Trogoderma* infestation in a warehouse the treatments were useless. Laboratory tests show that a local diatomite might be useful as an inert dust. Pyrethrum spread externally on sacks was of little use and DDT impregnated sacks failed against *Trogoderma*. Traps and heat treatments were not used.

Many local methods of handling groundnuts tend to spread *Trogoderma* but it seems unlikely that they can be easily eliminated. Routine preventative spraying must be supplemented by a rational programme of railing produce and by administrative changes to make *Trogoderma* infestation a disadvantage financially rather than an advantage.

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STUDIES ON AQUEOUS SUSPENSIONS OF INSECTICIDES.

PART III. FACTORS AFFECTING THE PERSISTENCE OF SOME SYNTHETIC INSECTICIDES.

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(Plates X–XII.)

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Introduction.

Studies on the toxicity of deposits from aqueous suspensions of DDT crystals have shown that there is an inverse relationship between particle size and effectiveness against mosquitos exposed for short contact periods (Hadaway & Barlow, 1951). Chemical determinations of the amounts of DDT picked up during the contact period and subsequently retained by mosquitos and tsetse flies confirm that the weight of insecticide acting on the insect and its rate of action are largely dependent on particle size. The smaller particles have a more rapid and greater toxic effect (Barlow & Hadaway, 1952).

The relationship between particle size and effectiveness is less marked with dieldrin and the gamma isomer of BHC than with DDT, DDD and methoxychlor. The former two compounds are intrinsically more toxic to mosquitos than are the other three, and the pick-up and retention of only a few crystals of these compounds may be lethal. It is also possible that the rate of penetration through the cuticle may be more rapid, enabling a lethal dose to be acquired from larger particles before they are dislodged.

It was thought that the persistence of insecticides, especially the more volatile ones, would be influenced by the initial size of the particles and that large particles which are the least effective, would persist longer than the small, effective particles. The persistence of crystals of different initial sizes applied to different types of materials was therefore studied.

It was found that the persistence of insecticides varied considerably on different materials. The most striking results were obtained with certain mud blocks. Crystals of all insecticides tested disappeared rapidly from the surface of mud blocks, and even crystals of DDT, which is usually regarded as a contact insecticide with a long residual effect, disappeared from the surface at 78°F. (25·5°C.) in a matter of days leaving the mud surface non-toxic to mosquitos. This remarkably rapid loss in toxicity on dried mud is of obvious importance in the control of adult mosquitos in houses where the walls are constructed of this material.

Materials and Methods.

Insecticides.

DDT	2,2-bis (p-chlorophenyl) 1,1,1-trichloroethane.
Gamma-BHC	Gamma isomer of hexachlorocyclohexane.
Aldrin	1,2,3,4,10,10-hexachloro-1,4,5,8-diendomethano-1,4,4a,5,8,8a-hexahydronaphthalene.
Dieldrin	The 6, 7 epoxy derivative of aldrin.

The physical properties of DDT, gamma-BHC and dieldrin have been given in a previous paper (Hadaway & Barlow, 1951). Aldrin used in this series had a melting point of 101–102°C. and a density of 1·73.

Preparation of formulations.

Insecticide crystals in different size ranges were obtained from ground samples as previously described. One small variation was the substitution of 0·2 per cent. for 0·1 per cent. Teepol as a suspending agent. It had been found that DDT and dieldrin could be kept without aggregation for longer periods in the stronger solution. Gamma-BHC and aldrin both showed a strong tendency to aggregation when suspended in a Teepol solution alone. The best medium was found to be a mixture of 0·5 per cent. Goulac and 0·2 per cent. Teepol although even using this it was best to stir the suspensions by high speed mechanical means before spraying and not to keep them too long after preparation.

Test surfaces.

Plaster blocks were prepared as previously described. Mud used for most of this work was a red lateritic soil from Uganda. It was made into circular blocks by mixing with sufficient distilled water to render it plastic and pressed into brass rings of the type used as moulds for plaster blocks. A smaller size was more convenient, for use in chemical tests. The two sizes of blocks were 44·5 and 14·8 sq. cm. in area, respectively, and had a common thickness of 1·2 cm. They were allowed to dry in the air at room temperature for several days and as used had a porosity of 37 per cent., identical with that of the plaster blocks. Applications of the insecticide suspensions were made in the tower described previously. A series of blocks were sprayed with an aqueous suspension of each formulation, and a fresh duplicate set was used for contact toxicity tests at each time interval after application. The same treated blocks were used throughout the fumigation tests. The treated blocks were stored in a large room except on a few occasions when it was possible to keep them at a controlled temperature.

Test insect.

Adult female mosquitos, *Aëdes aegypti* (L.), two to three days old and after one blood meal on guineapigs, were used throughout these experiments. Breeding techniques have been described previously (Hadaway and Barlow, 1949).

Exposure to treated surface.

Mosquitos were exposed for various contact periods to the treated surfaces by the " funnel " technique described and illustrated previously (Hadaway and Barlow, 1951).

Some compounds have a fumigant as well as a contact toxic action on insects. When insects are confined for a given time on a surface treated with one such compound their response may be due either to the contact or the fumigant effect or to a combination of both. Tests in which mosquitos were confined *on* treated surfaces under funnels are described throughout this paper as " contact " toxicity tests.

It is possible, however, to carry out tests in which insects are prevented from making contact with an insecticidal deposit in or on a treated material yet are exposed to the vapour given off from that deposit. The fumigant effect on the insects under these conditions is of necessity different from that when the insects are actually in contact with the surface, but it can be used as a measure of the persistence of the deposit. The fumigant action exerted by deposits was determined as follows :—

The apparatus consisted simply of a number of perspex cylinders each of which was 3 ins. in diameter and 3 ins. long. One end of each was closed with perspex except for a central aperture ½ in. in diameter, and the other end was covered with cotton mosquito gauze (mesh 45) held tautly in position by means of an elastic band. A perspex ring of the same diameter as the cylinder and ¼ in. in width was attached by means of adhesive tape to the end of the cylinder covered with gauze.

Thirty to forty mosquitos were blown gently from a sucking tube into each cylinder, through the central aperture in the perspex end of the cylinder and the aperture was then plugged with cotton wool. No carbon dioxide was used to facilitate the transference of mosquitos from stock cage to cylinder so that interference with their respiration was avoided. Inside the cylinder the majority of mosquitos preferred to rest on the cotton gauze. The perspex ring end of the cylinder was then fixed tightly against the treated surface which was clamped in a vertical position so that the cylinder was horizontal. Mosquitos in the cylinder were exposed, therefore, to vapour given off from the treated material yet were prevented from making direct contact with it by the cotton gauze ¼ in. from the surface.

At the end of the required exposure period the mosquitos in the cylinder were knocked down by a slow current of carbon dioxide and quickly transferred to a clean recovery cage. No significant differences in kills were obtained when mosquitos were transferred in this way and when they were transferred by sucking tube without anaesthesia. The cylinders and rings were cleaned thoroughly between tests and the cotton gauze discarded and replaced with new material.

All exposures were made at 78°F. and 60–70 per cent. relative humidity, and mosquitos were stored in a separate room under the same conditions for 24 hours before mortality counts were made. Recovery cages consisted of wire gauze cylinders, 3 ins. in diameter and 4 ins. in height, with detachable tin-plate ends. The base was lined with white filter paper and a plug of cotton wool soaked in sugar solution was inserted in a central aperture in the lid.

Fumigant Action of different Insecticides.

Mosquitos were exposed in perspex cylinders by the method just described to assess the initial fumigant effect exerted by different insecticides. The most potent fumigant was the gamma isomer of BHC, kills of mosquitos being obtained from low dosages. Aldrin, too, had a considerable fumigant effect, but that of dieldrin was comparatively slight and that of DDT was negligible. The results of some tests are given in Table I.

It may be of interest to record the behaviour of the mosquitos in the cylinders during exposures. After the initial restlessness on their introduction to the cylinder, the majority preferred to rest on the cotton gauze ¼ in. away from the treated surface rather than on the perspex cylinder itself. Mosquitos continued to rest on the cotton gauze even when the test surface had been treated at a high dosage with gamma-BHC, dieldrin, or aldrin, showing that the vapours of these insecticides are not apparently repellent to mosquitos. After resting on the gauze for a length of time, depending on the insecticide used, the mosquitos became active again and flew about in the cylinder, apparently normally at first and then with some unco-ordinated movements until they were finally knocked down. However, it was possible for mosquitos to die after exposure to fumigants even when they were transferred from the cylinder to a recovery cage before they were activated and before they were knocked down. For instance, in the tests with different dosages of gamma-BHC, results of which are given in Table I, no mosquitos were knocked down during the half-hour exposure yet 91 per cent. of the mosquitos exposed to the vapour from glass plates, treated at a dosage of 25 mg. per sq. ft., died.

TABLE I.

Fumigant action of different insecticides.

Insecticide	Surface treated	Dosage mg. per sq. ft.	Mean percentage kill in 24 hours after exposure of (hours)								
			0·25	0·5	0·75	1	2	3	4	5	6
Gamma-BHC	Glass	25	52	91							
		12·5	44	88							
		6	41	82							
		3	31	71							
		1	9	48							
Aldrin...	Glass	25		50		81					
Dieldrin	Glass	25						6	17		53
DDT ...	Glass	25									3
Aldrin...	Wallboard	100	33	68	90	100					
Dieldrin	Wallboard	100				7	43	90	96		
DDT ...	Wallboard	100							0		

Effect of Particle Size on Residual Toxicity.

At the beginning of this work it had only been intended to investigate the effect of particle size on residual effectiveness of the " volatile " insecticides, gamma-BHC and aldrin. As a matter of interest several surfaces were used in different experiments, results for which are presented in this section, and these demonstrated the great difference between mud and other materials. DDT, for instance, which as an insecticide has normally a very long life, was tested on mud, and the results showed that it too disappeared rapidly and that it was possible to show different rates of loss of the different sized particles.

DDT.

There was an initial inverse relationship between the size of DDT crystals sprayed in aqueous suspension on to mud blocks and their effectiveness against mosquitos exposed to them for short contact periods.

As would be expected the larger the particle the longer it persisted. Microscopical examination of the surface of mud blocks kept at 78°F. (25·5°C.) and at a relative humidity of 50 per cent. showed that particles in the 0–10 micron range were no longer visible two days after application, that those in the 10–20 micron range had disappeared by the end of the first week and those in the 20–40 micron range by the end of the second week. The contact toxicity of the blocks to mosquitos decreased at a corresponding rate (see Table II). No kills were obtained even after exposures of 128 minutes when particles were not visible on the surface.

Photographs of the surface of mud blocks at different times after their treatment at a dosage of 25 mg. DDT per sq. ft. are given in Plates X–XII.

TABLE II.

Initial and residual contact toxicity of DDT crystals at dosage of 25 mg. per sq. ft. on mud blocks kept at 78°F.

Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)									
		0·25	0·5	1	2	4	8	16	32	64	128
0–10 ...	1 hour	63	90	100	100						
	3 days							0	3	3	
	7 days								0	0	0
	14 days								0	0	0
10–20 ...	1 hour	33	58	90	100						
	3 days					0	33	85	100		
	7 days								0	3	38
	14 days								0	0	0
20–40 ...	1 hour			0	8	35	60				
	3 days					0	8	40	80		
	7 days							8	24	49	
	14 days								0	3	0

Aldrin.

The initial relationship between particle size and contact effectiveness was evident with crystals of aldrin on mud blocks, but to a lesser extent than with DDT. Crystals of aldrin in the smaller size ranges disappeared from the surface of mud blocks in a few hours even at a room temperature of 65–70°F., and only remnants of the larger crystals remained for 24 hours. Kills of mosquitos were obtained, however, even when crystals were no longer visible on the surface. One day after treatment, when some surface deposits remained on the blocks treated with large crystals, there was a reversal of the order of effectiveness and blocks sprayed with the largest crystals were most effective. All blocks were approximately equally effective three days after treatment, and after eight days those sprayed with particles larger than 40 microns were again less effective than those treated with smaller ones (see Table III).

TABLE III.

Initial and residual contact toxicity of aldrin crystals at dosage of 25 mg. per sq. ft. on mud blocks.

Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)								
		0·25	0·5	1	2	4	8	16	32	64
0–10	1 hour	100								
10–20	1 ,,	100								
20–40	1 ,,	100								
40–60	1 ,,	58	73							
60–80	1 ,,	10	29	63						
0–10	1 day					0	15	55		
10–20	1 ,,					0	15	55		
20–40	1 ,,					0	25	70		
40–60	1 ,,					15	55	90		
60–80	1 ,,					10	60	95		
0–10	3 days							0	35	95
10–20	3 ,,							0	40	100
20–40	3 ,,							10	49	100
40–60	3 ,,							5	50	100
60–80	3 ,,							10	43	98
0–10	8 days							0	8	78
10–20	8 ,,							0	10	78
20–40	8 ,,							0	10	90
40–60	8 ,,							0	3	68
60–80	8 ,,							0	0	40

Temperatures °F.

	Max.	Min.	Mean
1 day	70	66	68
3 days	70	61	66
8 ,,	72	60	66

The persistence of aldrin crystals of different sizes was also determined by measuring the fumigant effect on compressed wallboard kept at room temperature except when used for tests. Again there was an inverse relationship between the initial effectiveness and the size of the particles, this time because of the decrease in surface area with the increase in particle size for a given dosage and a corresponding decrease in the amount of insecticide vaporised in a given time. It is also evident from Table IV that the loss of effectiveness with time is more rapid with small crystals than with larger ones.

Gamma-BHC.

The initial relationship between particle size and effectiveness was not shown with particles of gamma-BHC on mud, all size ranges used giving 100 per cent. kills after only 15 seconds contact. This compound is more toxic to mosquitos than aldrin or DDT, and a lethal dose penetrates to the site of action even from the pick-up of a few large particles (Hadaway & Barlow, 1951).

Particles of gamma-BHC remained visible on the surface of mud blocks for a longer time than those of the corresponding size of aldrin. Again, the larger the particle the longer it persisted. Particles in the small size ranges had disappeared by the end of the first day at a temperature of 68°F.

TABLE IV.

Fumigant effect from aldrin crystals at dosage of 25 mg. per sq. ft. on wallboard.

Particle size	Age of deposit	Mean percentage kill in 24 hours after exposure of (hours)		
		1	2	3
0–10	1 hour	80		
10–20	1 ,,	77		
20–40	1 ,,	79		
40–60	1 ,,	52		
60–80	1 ,,	23		
0–10	1 day	50		
10–20	1 ,,	61		
20–40	1 ,,	73		
40–60	1 ,,	55		
60–80	1 ,,	31		
0–10	3 days	18	64	
10–20	3 ,,	31	75	
20–40	3 ,,	31	78	
40–60	3 ,,	36	70	
60–80	3 ,,	20	79	
0–10	8 days	0	0	13
10–20	8 ,,	0	4	23
20–40	8 ,,	0	7	25
40–60	8 ,,	0	10	36
60–80	8 ,,	0	0	22

TABLE V.

Initial and residual contact toxicity of gamma-BHC crystals at dosage of 25 mg. per sq. ft. on mud blocks.

Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)							
		0·25	0·5	1	2	4	8	16	32
0–10	1 hour	100							
10–20	1 ,,	100							
20–40	1 ,,	100							
40–60	1 ,,	100							
60–80	1 ,,	100							
0–10	1 day	0	3	8					
10–20	1 ,,	5	13	30					
20–40	1 ,,	8	18	50					
40–60	1 ,,	55	65	88					
60–80	1 ,,	53	56	83					
0–10	8 days						3	70	95
10–20	8 ,,						5	78	100
20–40	8 ,,						3	63	88
40–60	8 ,,						3	73	88
60–80	8 ,,						3	25	75
0–10	15 days						0	10	50
10–20	15 ,,						0	18	75
20–40	15 ,,						0	13	73
40–60	15 ,,						0	8	58
60–80	15 ,,						0	0	13

Temperatures °F.

	Max.	Min.	Mean
1 day ...	72	64	68
8 days ...	74	62	68
15 days ...	74	62	68

There was a marked loss in toxicity following the disappearance of particles from the surface, but, as with aldrin, kills of mosquitos were obtained in contact toxicity tests when no surface deposits were visible. One day after treatment the largest particles were the most effective, eight days after treatment all blocks were approximately equally effective, and after 15 days those treated with 60–80 micron particles were significantly less effective than the others (Table V).

Tests to determine the residual contact toxicity of gamma-BHC crystals of different sizes on plaster blocks showed that, as on mud, the rate at which they disappeared from the surface was dependent on their size, the smaller the crystal the more rapidly it disappeared. The particles persisted longer on the surface of plaster blocks than did those of the corresponding size on mud blocks. For instance, 10–20 micron crystals were no longer visible on the surface of mud blocks 24 hours after their application, yet were visible for nearly two weeks on plaster at a similar room temperature of 65–70°F. Kills of mosquitos were obtained when they were exposed to plaster blocks three weeks after treatment when the deposits of small crystals had disappeared from the surface. Some deposit could be seen on plaster blocks three weeks after they were sprayed with large crystals and these were more effective against mosquitos than were the blocks with no visible deposit from the smaller crystals. Results of one test are given in Table VI.

TABLE VI.

Initial and residual contact toxicity of gamma-BHC crystals at dosage of 25 mg. per sq. ft. on plaster blocks.

Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)						
		0·25	0·5	1	2	4	8	16
5–10 ...	1 day ...	100						
10–20 ...	1 „ ...	100						
20–40 ...	1 „ ...	100						
40–60 ...	1 „ ...	98						
60–80 ...	1 „ ...	93						
5–10 ...	1 week ...	95						
10–20 ...	1 „ ...	100						
20–40 ...	1 „ ...	100						
40–60 ...	1 „ ...	93						
60–80 ...	1 „ ...	78						
5–10 ...	2 weeks ...	18	63	85				
10–20 ...	2 „ ...	25	80	100				
20–40 ...	2 „ ...	20	83	100				
40–60 ...	2 „ ...	28	88	100				
60–80 ...	2 „ ...	28	75	100				
5–10 ...	3 weeks ...					0	18	83
10–20 ...	3 „ ...					5	23	98
20–40 ...	3 „ ...					0	25	100
40–60 ...	3 „ ...					10	40	100
60–80 ...	3 „ ...					38	85	100

Temperatures °F.

	Max.	Min.	Mean
1 day	68	60	65
1 week	68	56	60
2 weeks	80	56	66
3 weeks	80	56	66

Gamma-BHC in different particle sizes was also sprayed on to compressed wallboard and its residual effectiveness followed by fumigant tests as was described for aldrin. The results are given in Table VII and are similar to those obtained with aldrin (Table IV). With both aldrin and gamma-BHC there is a much greater persistence of solid particles on the surface of wallboard than on that of mud.

TABLE VII.

Fumigant effect from gamma-BHC crystals at dosage of 25 mg. per sq. ft. on wallboard.

Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (hours)						
		0·25	0·5	0·75	1	2	3	4
5–10	1 day	52	96	100				
10–20	1 ,,	44	86	100				
20–40	1 ,,	40	74	100				
40–60	1 ,,	18	52	95				
60–80	1 ,,	7	50	88				
5–10	1 week	46	94	100				
10–20	1 ,,	43	85	100				
20–40	1 ,,	30	70	95				
40–60	1 ,,	18	50	88				
60–80	1 ,,	15	43	79				
5–10	3 weeks				6	60	100	
10–20	3 ,,				6	61	100	
20–40	3 ,,				3	53	86	
40–60	3 ,,				3	43	80	
60–80	3 ,,				5	41	88	
5–10	4 weeks				6	54	95	
10–20	4 ,,				3	54	98	
20–40	4 ,,				5	48	86	
40–60	4 ,,				0	31	86	
60–80	4 ,,				0	33	86	
5–10	8 weeks						18	52
10–20	8 ,,						32	62
20–40	8 ,,						23	50
40–60	8 ,,						11	41
60–80	8 ,,						6	30

Variation in Persistence of Gamma-BHC on different Materials.

It will be seen from some of the foregoing results that the persistence of a given particle size varied with the surface to which it was applied. Also that different surfaces showed different relative rates of loss at various times after application. To confirm this 10–20 micron gamma-BHC particles were sprayed on to different materials and the residual action of the deposits compared by fumigation tests at intervals afterwards.

Mud, plaster, wallboard and glass.

There was a marked reduction in effectiveness following the disappearance of crystals from the surface of mud blocks during the first day after application but the blocks continued to exert a fumigant effect at a reduced level for many weeks. In contrast, crystals remained visible on glass plates for a period of more than two weeks and the fumigant effect decreased only slowly but when, after four weeks, no deposits were visible the fumigant effect was negligible.

Deposits persisted for a longer time on plaster and wallboard than on mud but for a shorter time than on glass. There was a fumigant effect from these materials after the disappearance of surface deposits but this was less persistent than that from mud blocks. Results are given in Table VIII.

TABLE VIII.

Fumigant effect from 10–20 micron gamma-BHC crystals at dosage of 25 mg. per sq. ft. on different materials.

Material	Age of deposit	Mean percentage kill in 24 hours after exposure of (hours)									
		0·125	0·25	0·5	0·75	1	2	3	4	5	6
Mud ...	1 hour ...	0	17	53							
	1 day ...		0	7		36	83				
	8 days ...					0	23	63			
	2 weeks					0	18	51			
	4 weeks						10	42	71		
	6 weeks						5	28	52		
Plaster ...	1 hour ...	6	39	73							
	1 day ...	3	31	69							
	8 days ...		4	29	75						
	2 weeks				4	23	59				
	4 weeks						4	17	48		
	6 weeks								1	6	16
Wallboard	1 hour ...	3	32	68							
	1 day ...	0	29	65							
	8 days ...		0	16	58						
	2 weeks			3	20	49					
	4 weeks					3	37	80			
	6 weeks						1	22	62		
Glass ...	1 hour ...	7	40	83							
	1 day ...	3	33	72							
	8 days ...		9	63	92						
	2 weeks			24	61	94					
	4 weeks					0	2	9			
	6 weeks								0	0	0

Other porous materials.

Comparisons on other porous materials showed that the visible persistence of 10–20 micron gamma-BHC crystals on cement blocks and on unglazed porcelain tiles was similar to that on plaster blocks, and was much greater than that on mud blocks.

Comparative Residual Toxicities of Insecticides.

The preceding experiments had indicated the general effects of particle size and surface treated on residual effectiveness. Opportunity was now taken to compare the relative residual toxicities of different members of the four insecticides used in single experiments so that the conditions under which they were kept and tested would be identical in every respect. To broaden the scope of the experiments, different surfaces were also used to stress the previous indications of varying degrees of sorption by the absorbent surfaces and subsequent continued insecticidal effects by those insecticides capable of exerting a fumigant action. In particular, the experiment whose results are given in Table XII was designed to show these interactions fully.

It is essential that insecticides should be in the same physical state and be equally available to insects when their potencies are compared. The following contact toxicity tests were carried out with deposits from aqueous suspensions of 10–20 micron crystals.

Aldrin and gamma-BHC on mud and plaster.

Gamma-BHC was more effective against mosquitos and had a longer residual life than aldrin on both mud and plaster. Surface deposits of both insecticides persisted for a longer time on plaster than on mud. Kills of mosquitos were obtained after the disappearance of the deposits from both materials. Details of the results are given in Table IX.

TABLE IX.

Residual contact toxicity of 10–20 micron crystals of aldrin and gamma-BHC at a dosage of 25 mg. per sq. ft. on mud and plaster blocks.

Insecticide	Surface	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)								
			0·25	0·5	1	2	4	8	16	32	64
Aldrin	Mud	1 hour ...	100								
		1 day ...					0	15	55		
		3 days ...							0	40	100
		8 days ...							0	10	78
Aldrin	Plaster... ...	1 hour ...	98								
		1 day ...	100								
		3 days ...						33	93	100	
		8 days ...							10	55	100
Gamma-BHC ...	Mud	1 hour ...	100								
		1 day ...	5	23	45	78					
		8 days ...						5	63	100	
		15 days ...						0	10	55	98
Gamma-BHC ...	Plaster... ...	1 hour ...	100								
		1 day ...	98								
		8 days ...	85	100							
		15 days ...		0	10	50					

Temperatures °F.

	Max.	Min.	Mean
1 day ...	70	66	68
3 days ...	70	61	66
8 days ...	72	60	66
15 days ...	72	59	65

Dieldrin and gamma-BHC on mud and plaster.

Particles of both insecticides persisted for a much longer time on plaster than on mud. Particles of dieldrin were still present twelve weeks after their application to plaster blocks, and 100 per cent. kills were obtained after brief exposures of 15 seconds contact. Very little could be seen on the plaster blocks two weeks after their treatment with gamma-BHC. The toxicity of these blocks decreased rapidly after the disappearance of surface deposits.

Dieldrin crystals remained visible on mud blocks for less than two weeks ; gamma-BHC crystals for approximately one day only. No kills were obtained following the disappearance of dieldrin crystals but the blocks remained toxic for many weeks after the disappearance of gamma-BHC crystals. Seven weeks after treatment with gamma-BHC the mud blocks were more toxic than the plaster blocks. Results of this test are given in Table X.

TABLE X.

Residual contact toxicity of 10–20 micron crystals of dieldrin and gamma-BHC at a dosage of 25 mg. per sq. ft. on mud and plaster blocks.

Insecticide	Surface	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)									
			0·25	0·5	1	2	4	8	16	32	64	128
Dieldrin ...	Mud ...	1 hour ...	100									
		1 day ...	100									
		1 week ...	0	0	10	35	80					
		2 weeks...					0	0	0			
Dieldrin ...	Plaster ...	1 hour ...	100									
		1 week ...	100									
		2 weeks...	100									
		4 weeks...	100									
		7 weeks...	100									
		12 weeks...	100									
Gamma-BHC ...	Mud ...	1 hour ...	100									
		1 day ...	30	65	100							
		1 week ...					3	38	76			
		2 weeks...							13	74	100	
		4 weeks...							3	55	100	
		7 weeks...							0	38	93	
		12 weeks...								18	70	100
Gamma-BHC ...	Plaster ...	1 hour ...	100									
		1 week ...	100									
		2 weeks...	33	88	100							
		4 weeks...					3	30	80			
		7 weeks...							0	13	68	
		12 weeks...								0	3	28

Temperatures °F.

	Max.	Min.	Mean
1 day ...	62	59	60
1 week ...	67	53	60
2 weeks ...	68	50	60
4 weeks ...	68	49	58
7 weeks ...	68	40	55
12 weeks ...	70	38	54

DDT, dieldrin and gamma-BHC on mud.

Results similar to those obtained in the previous experiment were obtained with dieldrin and gamma-BHC on mud blocks kept at room temperature. Temperatures were rather lower than during the previous test and surface deposits persisted for a slightly longer time. DDT was initially less effective than either dieldrin or gamma-BHC but crystals remained on the surface of mud blocks for a much longer time than either of these compounds and DDT particles were still visible four weeks after application. After eight weeks, however, only a trace of DDT could be seen on the surface and kills were negligible (see Table XI).

TABLE XI.

Residual contact toxicity of 10–20 micron crystals of DDT, dieldrin and gamma-BHC at a dosage of 25 mg. per sq. ft. on mud blocks.

Insecticide	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)								
		0·25	0·5	1	2	4	8	16	32	64
DDT	1 hour ...	5	26	66	95					
	1 week ...	8	33	60	95					
	2 weeks ...	0	10	40	78					
	4 weeks ...		0	8	25	40				
	8 weeks ...							0	0	18
Dieldrin ...	1 hour ...	100								
	1 day ...	100								
	5 days ...	98								
	1 week ...	10	45	75	95					
	2 weeks ...						18	55	68	
	4 weeks ...						0	0	10	43
	8 weeks ...							0	0	0
Gamma-BHC...	1 hour ...	100								
	1 day ...	20								
	5 days ...			3	8	58	95			
	1 week ...					10	49	85		
	2 weeks ...						5	38	88	
	4 weeks ...							20	63	100
	8 weeks ...							0	18	78

Temperatures °F.

	Max.	Min.	Mean
1 day ...	64	60	62
5 days ...	66	40	53
1 week ...	66	40	55
2 weeks ...	67	40	54
4 weeks ...	70	38	53
8 weeks ...	70	34	51

DDT, dieldrin and gamma-BHC on mud, plaster and glass.

Aqueous suspensions of 10–20 micron particles of DDT, dieldrin and gamma-BHC were sprayed at a dosage of 25 mg. per sq. ft. on to mud and plaster blocks and glass plates which were kept at a constant temperature of 78°F. and relative humidity of 50 per cent.

Results obtained with mud blocks were similar to those in the previous experiment except that volatilisation took place much more rapidly than at the lower room temperatures. Gamma-BHC crystals disappeared from the surface in approximately three hours, and there was a marked reduction in effectiveness when mosquitos were exposed one day after spraying. The loss in toxicity was then more gradual

TABLE XII.

Residual contact toxicity of 10–20 micron crystals of DDT, dieldrin and gamma-BHC at a dosage of 25 mg. per sq. ft. on mud, plaster and glass kept at 78°F.

Material treated	Insecticide	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)									
			0·25	0·5	1	2	4	8	16	32	64	128
Mud	DDT ...	1 hour ...	22	54	85	100						
		1 day ...	13	35	58	93						
		3 days ...				0	8	30	64	98		
		1 week ...							0	0	0	
	Dieldrin ...	1 hour ...	100									
		1 day ...	45		60	78						
		3 days ...					0	0	0	3	0	
		1 week ...								0	0	3
	Gamma-BHC	1 hour ...	100									
		1 day ...			0	8	40	80				
		3 days ...						13	30	75		
		1 week ...							8	43	95	
		2 weeks ...							0	20	60	
		4 weeks ...								3	40	100
		8 weeks ...								0	25	78
Plaster ...	DDT ...	1 hour ...	26	60	85	100						
		1 week ...		73	93	100						
		2 weeks ...	30	62	90	100						
		4 weeks ...	33	55	75	100						
		8 weeks ...	20	45	68	95						
	Dieldrin ...	1 hour ...	100									
		1 week ...	100									
		2 weeks ...	66	98	100							
		4 weeks ...	0			10	38	70	95			
		8 weeks ...							5	37	78	
	Gamma-BHC	1 hour ...	100									
		1 day ...	100									
		3 days ...	90									
		1 week ...			0	18	55	80				
		2 weeks ...							7	38	83	
		4 weeks ...								0	34	93
		8 weeks ...								0	3	28
Glass	DDT ...	1 hour ...					8	20	63			
		1 week ...					5	15	55			
		2 weeks ...					5	25	67			
		4 weeks ...					0	15	65			
	Dieldrin ...	1 hour ...	25	54	83							
		1 week ...	8		55	85						
		2 weeks ...	5		48	85						
		4 weeks ...	10		65	90						
	Gamma-BHC	1 hour ...	18	43	73							
		1 week ...	0		0	10	38					
		2 weeks ...						0	0	15		
		3 weeks ...								0	15	77
		4 weeks ...								0	0	35

and blocks were still effective against mosquitos exposed for a period of 128 minutes eight weeks after spraying. Dieldrin particles were no longer visible on the surface on the third day after application. DDT particles were more persistent and some deposit remained visible on the surface for about five days. Blocks treated with dieldrin and DDT were, however, non-toxic to mosquitos exposed to them for periods of up to 128 minutes one week after treatment.

The visible persistence of all three insecticides was greater on plaster than on mud blocks. Gamma-BHC particles remained on the surface of plaster blocks for four to five days. The blocks retained some toxicity after the disappearance of surface deposits but loss of toxicity was subsequently more rapid than on mud and after four weeks mud blocks were more effective than plaster blocks. Although deposits on plaster blocks sprayed with dieldrin crystals were appreciably less after four weeks some particles remained and kills were obtained after exposures of from two to 16 minutes. Plaster blocks sprayed with DDT crystals showed little change visually or in toxicity after eight weeks.

All insecticides were less effective on glass plates than on mud or plaster blocks. The wetting agent solution remains with the insecticide particles on non-porous plates and on drying, causes them to adhere strongly to the surface so that they cannot be picked up so readily as from a porous material. Kills after 16 minutes contact with DDT particles on glass were similar to those after 0·5 minutes on plaster. Initially dieldrin and gamma-BHC were approximately equally effective on glass. Gamma-BHC particles persisted for a longer time on glass than on mud or plaster. On glass there is no loss by sorption, and the wetting agent solids probably retard evaporation.

Results of this test are given in Table XII.

Commercial Formulations on different Materials.

The following experiments were carried out to compare the behaviour of commercial formulations of insecticides with that of the pure materials.

DDT formulations.

A commercial wettable powder containing DDT particles with a mean size of 24 microns and an oil-bound suspension containing DDT crystals with a mean size of 10–12 microns, both behaved in the same way as the pure material on mud blocks at 78°F. Toxicity to mosquitos in contact with the treated surfaces decreased markedly during the first week, and after two weeks no kills were obtained after contact periods of up to 128 minutes. This test was carried out at the same time as that on the persistence of DDT crystals of different sizes, and the results given in Table XIII are strictly comparable with those given in Table II.

TABLE XIII.

Initial and residual contact toxicity of commercial DDT formulations at a dosage of 25 mg. DDT per sq. ft. on mud blocks kept at 78°F.

Formulation	Particle size in microns	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)									
			0·25	0·5	1	2	4	8	16	32	64	128
Wettable powder	24	1 hour ...			5	20	60	90				
		3 days ...					0	18	54	90		
		7 days ...							0	13	35	
		14 days ...								0	3	0
Oil-bound suspension	10–12 ...	1 hour ...	28	63	93	100						
		3 days ...					0	10	35	83		
		7 days ...							0	3	20	
		14 days ...								0	0	0

A dosage of 25 mg. DDT per sq. ft. is convenient for use in laboratory tests but is lower than that used in the field. The duration of effectiveness of deposits from aqueous suspensions of commercial wettable powders at dosages of 100, 200 and 400 mg. DDT per sq. ft. on mud blocks stored at 78°F. was therefore investigated. A 75 per cent. DDT wettable powder containing DDT particles with a mean size of 6 microns, and a 50 per cent. powder containing DDT particles with a mean size of 24 microns were used.

Deposits from the wettable powder containing the larger particles of insecticide were less effective initially, but retained a degree of effectiveness for a longer period. It was noticeable that, at these higher dosages, superimposition and aggregation of particles occurred and that clusters of particles persisted for a longer time than the single crystals at the lower dosage of 25 mg. per sq. ft. Even so, dosages as high as 400 mg. DDT per sq. ft. were relatively ineffective after eight weeks and the mosquitos walked over the surface of the mud for as long as one hour before acquiring a lethal dose of insecticide. The results of this test are given in Table XIV.

Gamma-BHC formulations.

The relative persistence of deposits from aqueous suspensions of a commercial wettable powder P.520 containing 50 per cent. crude benzene hexachloride (*i.e.*,

TABLE XIV.

Initial and residual contact toxicity of commercial DDT wettable powders at high dosages on mud blocks kept at 78°F.

Formulation	Age of deposit	Dosage, mg. DDT per sq. ft.	Mean percentage kill in 24 hours after exposure of (minutes)								
			0·25	0·5	1	2	4	8	16	32	64
75% wettable powder, particles mean size of 6 microns	1 day	100	100								
		200	100								
		400	100								
	1 week	100			30						
		200			95						
		400			100						
	4 weeks	100				0	0	0			
		200				0	5	13			
		400				51	77	100			
	8 weeks	100							0	0	0
		200							0	0	3
		400							0	18	66
50% wettable powder, particles mean size of 24 microns	1 day	100					82				
		200					75				
		400					85				
	1 week	100					40				
		200					55				
		400					75				
	4 weeks	100					0	0	0		
		200					0	2	70		
		400					10	31	98		
	8 weeks	100							0	0	5
		200							0	20	80
		400							12	72	100

6·5 per cent. gamma isomer) on a number of materials was similar to that of pure crystals in both contact toxicity and fumigation tests. The results of one fumigation test are given in Table XV. There was a marked loss in effectiveness on mud during the first day and then a more gradual loss. On the other hand, the effectiveness on aluminium plates decreased only slightly at first and then very rapidly. Deposits on thatch made from wheat-stem straw appeared to behave in the same way as those on non-porous metal plates.

TABLE XV.

Fumigant effect from P.520 at a dosage of 100 mg. BHC per sq. ft. (13 mg. gamma isomer) on different materials.

Material	Age of deposit	Mean percentage kill in 24 hours after exposure of (hours)					
		0·25	0·5	1	2	3	4
Mud	1 hour ...	8	42				
	1 day ...		0	22	61		
	1 week ...				18	54	
	2 weeks ...					10	31
Plaster	1 hour ...	23	60				
	1 day ...	19	49	95			
	1 week ...			12	52		
	2 weeks ...					10	65
Wallboard	1 hour ...	27	61				
	1 day ...	12	37	90			
	1 week ...			7	44		
	2 weeks ...					44	87
Wood	1 hour ...	27	58				
	1 day ...	21	53	95			
	1 week ...			17	60		
	2 weeks ...					13	57
Thatch	1 hour ...	46	80				
	1 day ...	35	68				
	1 week ...			13	52		
	2 weeks ...					8	37
Aluminium	1 hour ...	49	89				
	1 day ...	40	79				
	1 week ...			5	41		
	2 weeks ...					3	19

The persistence of 10–20 micron gamma-BHC crystals on mud blocks was compared with that of similar crystals mixed with an inert diluent (speswhite kaolin) to give a wettable powder containing 13 per cent. gamma-BHC, with impregnated dusts and with a 5 per cent. kerosene solution. Impregnated dusts were made by dissolving the insecticide in ether and mixing the solution with enough inert dust to give a powder containing 25 per cent. by weight of insecticide. Air was blown over the surface of the mixture which was continuously ground as the ether evaporated. The powder was suspended in 0·5 per cent. Teepol for spraying.

It can be seen from the results given in Table XVI that although the kerosene solution was absorbed into the mud and kills were lower than with the other formulations there was a persistent toxic effect but also at a lower level than with the other formulations. All the other formulations remained equally effective.

TABLE XVI.

Residual contact toxicity of gamma-BHC formulations at dosage of 25 mg. gamma-BHC per sq. ft. on mud blocks.

Formulation	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)								
		0·25	0·5	1	2	4	8	16	32	64
10–20 micron crystals	1 hour...	100								
	2 days...	28								
	1 week...					10	55	95		
	2 weeks						5	51	85	
	5 weeks						0	27	75	
	8 weeks							0	17	83
10–20 micron crystals + spes-white	1 hour...	100								
	2 days...	40								
	1 week...					13	55	98		
	2 weeks						10	60	88	
	5 weeks						0	28	73	
	8 weeks							0	17	78
Impregnated diatomite	1 hour...	100								
	2 days...	43								
	1 week...					23	78	100		
	2 weeks						13	56	90	
	5 weeks						0	34	85	
	8 weeks							0	10	68
Impregnated slate dust	1 hour...	100								
	2 days...	64								
	1 week...					28	90	100		
	2 weeks						10	60	93	
	5 weeks						0	40	83	
	8 weeks							0	20	83
Kerosene solution	1 hour...			0	23	73	100			
	2 days...						19	54	98	
	1 week...						13	38	93	
	2 weeks						0	25	63	
	5 weeks							3	40	88
	8 weeks							0	0	33

Aldrin formulations.

Results obtained on plaster blocks with aqueous suspensions of aldrin crystals, wettable powder, and impregnated dusts showed that, as with gamma-BHC, there was little variation in their persistence.

Summary of Residual Tests.

The outstanding features of all experiments can be listed as follows :—

1. Particles of all four insecticides, DDT, gamma-BHC, dieldrin and aldrin, disappear very rapidly from the surface of mud blocks at dosages of 25 mg. per sq. ft.

2. When surface deposits of DDT and dieldrin are no longer visible on mud blocks, negligible kills are obtained even after comparatively long contact exposures.

3. There is a marked loss in " contact " toxicity on mud blocks following the disappearance of surface deposits of aldrin and gamma-BHC, but the toxic effect at a reduced level persists for many weeks.

4. Particles of all insecticides remain for a much longer time on plaster blocks and wallboards than on mud blocks. Plaster blocks and wallboards also retain some

toxicity to mosquitos after the disappearance of crystals of aldrin and gamma-BHC from the surface, but this toxicity is lost more rapidly than it is on mud blocks.

5. Particles of gamma-BHC and aldrin persist for a longer time on glass plates than on mud blocks but, as soon as they disappear from the surface, toxicity is lost completely.

6. Aldrin and gamma-BHC have a marked fumigant effect on mosquitos ; DDT and dieldrin have not.

It is clear that the fumigant properties of aldrin and gamma-BHC are important in the interpretation of these results. Further experiments were carried out to confirm this and to explain the remarkable results obtained on mud.

Chemical Tests on Sorption by Mud.

Method.

pp′ DDT was determined by a modification of the Schechter-Haller method described by Barlow and Hadaway (1952). The insecticide was recovered from whole blocks ground to a fine powder, or from separate layers. The latter were obtained by scraping with a scalpel until a given weight of mud had been removed. Some contamination of the next layer cannot be avoided by this method, of course, but as can be seen by reference to Table XVII such contamination is not more than about 10 per cent. as shown by the figures for samples taken immediately after spraying. The powdered samples of mud were extracted in a Soxhlet apparatus with benzene for four hours, the extract made up to 50 ml. and a suitable aliquot taken from it for analysis. Extracts from unsprayed mud gave blank colours and DDT concentrations derived from the colorimeter readings were corrected for this interference.

Preliminary tests.

The first estimations made were merely to determine the fate of DDT which had disappeared from the surface of mud blocks. Two large blocks, sprayed with 10–20 micron DDT particles at 25 mg. per sq. ft. (equivalent to 1·2 mg. per block) were kept at 25°C. and 50 per cent. relative humidity for one week, after which time crystals were not visible on the surface and mosquitos exposed to the blocks for long contact periods were not killed. Each block was ground and extracted and yielded 1·2 and 1·3 mg. DDT respectively, indicating that all the dosage applied had been recovered. The absorption curves of the colours developed in the analysis were identical with that of pure pp′ DDT.

Additional evidence that DDT was unchanged after sorption was obtained from nine mud blocks which had been sprayed six weeks previously at 100 mg. per sq. ft., three with 0–10, three with 10–20 and three with 20–40 micron DDT crystals. They had been tested biologically against mosquitos after the disappearance of surface deposits and no kills had been obtained after exposures of 64 minutes. The blocks were powdered and extracted with petroleum ether in a Soxhlet apparatus. On removal of the solvent from the extract a residue was obtained which, on the basis of a labile chlorine estimation, indicated a recovery of about 90 per cent. of the DDT originally sprayed on to the blocks. This residue, which amounted to 90 mg. containing about 40 mg. DDT, was purified from impurities extracted from the mud by chromatography on alumina and crystallisation from ethanol. After three re-crystallisations the product weighed 10 mg., had a melting point of 106–107°C. did not depress the melting point of pure pp′ DDT and contained 9·8 per cent. chlorine removable by alcoholic potassium hydroxide.

Complete recovery of gamma-BHC from the interior of mud blocks was also demonstrated through the kind collaboration of Drs. Armstrong and Bradbury of Imperial Chemical Industries, Ltd. Sensitive methods for determination of aldrin and dieldrin were not available, but it is reasonable to suppose that they were sorbed in the same way as DDT and gamma-BHC.

Change of distribution of insecticide with time.

Three small blocks were sprayed with 10–20 micron DDT crystals at 25 mg. per sq. ft. (equivalent to 0·4 mg. per block). At intervals one was taken and the superficial layer, 0·25 gm. weight, of the sprayed surface removed. This was approximately 0·01 cm. thick. The rest of the block was then ground and the two samples extracted. Changes in distribution shown by the figures in Table XVII may be compared with the photomicrographs of 10–20 micron crystals on Plates X–XII. It will be appreciated that as the crystals outside cannot be removed alone without a finite layer of mud a certain amount of DDT is recovered from the superficial layer even when the crystals have disappeared visually from the surface.

TABLE XVII.

Recoveries of DDT from mud blocks at different times after spraying with 10–20 micron crystals.

Days after application	Position of sample	µg. DDT recovered
0	Superficial layer Remainder	430 40
2	Superficial layer Remainder	200 200
7	Superficial layer Remainder	90 310

Distribution within the block.

One small block sprayed 11 days previously with 10–20 micron DDT crystals at 25 mg. per sq. ft. was divided into 5 equal layers. Each layer weighed 5·6 gm. and was about 0·225 cm. in thickness. Recoveries of DDT from these layers were as follows :—

Layer No. :—	1	2	3	4	5
µg. DDT :—	400	16	10	5	0

Therefore, practically all of the sorbed DDT was in the top fifth of the block.

A further block was treated with a much higher dosage to see if the distribution changed appreciably. On this occasion the superficial layer was first removed and the remainder of the block divided into five layers. The DDT recovered was equivalent to 275 mg. per sq. ft.

Layer :—	Superficial	1	2
µg. DDT :—	700	3,650	negligible

Even with this high dosage most of the sorbed DDT was near the surface.

Three further blocks were sprayed at intermediate dosages and sampled as follows :—superficial layer 0·25 gm., followed by layers 1, 2, 3 and 4 of 1·0 gm. each. The rest of the block was not used. 1·0 gm. is equivalent to a depth of approximately 0·04 cm. It can be seen from the results given in Table XVIII that even at high dosages the concentration of sorbed DDT decreased quite rapidly from the surface downwards and there was no sign that the outer layers of the mud were saturated. In each layer the DDT recovered was proportional to the dosage.

TABLE XVIII.

Recoveries of DDT from mud blocks sprayed with different dosages of 10–20 micron crystals.

Total dosage recovered mg. per sq. ft.	Microgrammes DDT in each layer				
	Superficial	1	2	3	4
48	153	350	160	85	12
77	260	620	220	100	19
189	570	1,500	610	300	55

The effect of increasing dosage upon the rate of disappearance of DDT particle was observed visually in the above experiments. So long as there is only a single layer of particles on the surface the rate does not change, but when superimposition takes place the piles of particles have a longer residual life than the single layer.

Work has started on ways of preventing this rapid loss of insecticide on mud and some preliminary results will be mentioned briefly.

It can be seen from the experiment described on page 303 under the heading " Some features of the sorption process " that the rate of loss of a layer of gamma-BHC on mud is greatly reduced by interposing a layer of filter paper between it and the mud. It was therefore thought that a layer of limewash such as may be encountered in practice might have the same effect.

Two small mud blocks were painted with a thin suspension of limewash and allowed to dry for one week. They and two unlimed blocks were sprayed with 10–20 micron DDT crystals at 50 mg. per sq. ft. After 1 and 2 weeks one block of each type was sampled by the usual method, taking a superficial layer of 0·25 gm. and a layer immediately beneath of 5·0 gm. weight. It can be seen from the results in Table XIX that the presence of the lime layer does delay the sorption process to some extent and probably a thicker layer of lime may be even more effective.

When wettable powders are used at higher dosages, the presence of larger amounts of inert diluent might have an effect similar to that provided by a layer of limewash by removing the DDT particles away from the surface of the mud. Therefore two mud blocks were sprayed with 10–20 micron DDT particles at 150 mg. per sq. ft. and two more with the same amount of DDT mixed with an equal quantity of speswhite china clay. The blocks were again sampled to remove the superficial layer and the layer immediately below of 0·25 and 5·0 gm. respectively. From the

TABLE XIX.

The effect of inert materials on the sorption of DDT by mud.

Time in weeks after application	Surface or formulation used	% of DDT recovered in	
		(*a*) outer layer	(*b*) inner layer
1	Mud, alone	24	76
	Mud, limewashed	63	37
2	Mud, alone	15	85
	Mud, limewashed	41	59
1	DDT, alone	35	65
	DDT, with china clay ...	44	56
2	DDT, alone	20	80
	DDT, with china clay ...	24	76

results in Table XIX it is obvious that the presence of a diluent had only a slight effect on the rate of loss from the surface.

The mud blocks used in these two experiments were of rather different composition from those normally used and the rate of loss of the higher dosages was rather less than that normally encountered with Uganda mud.

Further Biological Tests.

It has been shown above that the insecticide lost from the surface is present in the block. The following tests were carried out to show that only insecticides with a marked fumigant action could exert a toxic effect after sorption.

Tests on scraped mud blocks.

When no surface deposits were visible on blocks sprayed with 10–20 micron crystals of DDT and dieldrin at a dosage of 25 mg. per sq. ft. no kills were obtained when mosquitos were exposed to the surfaces for contact periods of 128 minutes. The outer layer of 0·01 cm. thickness was removed from each block and mosquitos were exposed to the new surfaces for 128 minutes. Again, no kills were obtained.

When no surface deposits were visible on blocks sprayed with 10–20 micron gamma-BHC crystals at a dosage of 25 mg. per sq. ft. a mean kill of 75 per cent. was obtained after a contact period of 32 minutes. Exposures to the new surfaces for the same period following the removal of a layer of 0·01 cm. thickness resulted in a mean kill of 88 per cent. Removal of 0·23 cm. from each block reduced the kill after a contact period of 32 minutes to 23 per cent.

This suggests that the sorbed insecticide is not readily available for pick-up, for although dieldrin and gamma-BHC are equitoxic to mosquitos only the latter was toxic after sorption.

It is of interest to note here the behaviour of the mosquitos on mud blocks after the disappearance of surface deposits of gamma-BHC. After the initial restlessness they settled down on the surface and remained stationary for about 25 minutes in this test, and then became active again and walked over the surface. Transference to recovery cages after 32 minutes resulted in a mean kill of 75 per cent. This behaviour is very similar to that occurring in fumigation tests described previously.

Tests with kerosene solutions.

Absorption is known to occur when kerosene solutions of DDT are sprayed on to mud blocks, and the resulting surface deposits are small and relatively ineffective against mosquitos (Hadaway & Barlow, 1949). Five per cent. solutions of DDT, dieldrin and gamma-BHC in kerosene were sprayed on to mud blocks at a dosage of

TABLE XX.

Toxicity of mud blocks sprayed with 5 per cent. kerosene solutions at a dosage of 25 mg. insecticide per sq. ft.

Insecticide	Mean percentage kill in 24 hours after exposure of (minutes)			
	4	8	16	32
DDT		0	0	0
Gamma-BHC ...	3	35	83	100
Dieldrin		0	0	0

Blocks kept at 62°F. for 24 hours after application.

25 mg. insecticide per sq. ft. It will be seen from the results given in Table XX that only the blocks sprayed with gamma-BHC were effective against mosquitos exposed to the surfaces for contact periods of up to 32 minutes. This again suggests that the toxicity obtained is due to a fumigant effect from the material inside the blocks.

Exposures at different temperatures.

Exposures of mosquitos were made to a series of mud blocks when no surface deposits were visible eight days after their treatment with 10–20 micron gamma-BHC crystals at a dosage of 25 mg. per sq. ft., first at a temperature of 65°F. and then at 78°F. The kills obtained are given in Table XXI and were higher when the exposures were made at 78°F. than at 65°F., suggesting that there is a more rapid diffusion of vapour from the material inside the blocks at the higher temperature.

TABLE XXI.

Effect of temperature of exposure on toxicity of mud blocks 8 days after spraying with 10–20 micron gamma-BHC crystals at a dosage of 25 mg. per sq. ft.

Temperature of exposure	Mean percentage kill in 24 hours after exposure of (minutes)			
	4	8	16	32
65°F.		3	28	70
78°F.	5	43	78	
Untreated at 65°F.			0	0
,, ,, 78°F.			0	0

Some features of the sorption process.

It appears from previous results that sorption of some insecticides by mud occurs very rapidly but that desorption, as shown by the prolonged effect from gamma-BHC-treated blocks, is very much slower. The following experiment compares sorption and desorption rates on mud and plaster, and shows that sorption occurs from the vapour phase of gamma-BHC. The relative effects of different surfaces on rates of disappearance of particles are similar with each insecticide used and the physical mechanisms involved are presumably the same in each case. Gamma-BHC was used in this experiment because interposing filter paper between the insecticide particles and the mud surface increases the residual life by roughly 20 times. This difference would make a similar experiment with DDT inconveniently long.

Circles of filter paper were sprayed with aqueous suspensions of 10–20 micron gamma-BHC crystals at a dosage of 25 mg. per sq. ft. and were placed flat on the surface of untreated plaster and mud blocks and glass plates. The treated surface of each filter paper was placed uppermost so that the deposit was separated from the untreated materials by the thickness of the paper. They were stored at 78°F. and 50 per cent. relative humidity.

Filter papers were removed from some of the blocks and plates one day after treatment and mosquitos were exposed to them and to the blocks. The blocks were then kept at the same temperature without the papers, and mosquitos exposed to them after further time intervals. The same procedure was adopted with other blocks except that the papers were allowed to remain on some for two days and on others for three days.

The toxicity of filter papers on mud blocks decreased more rapidly than did that of papers on plaster blocks. Filter papers on glass still gave 100 per cent. kills after 15 seconds contact three days after treatment, see Table XXII. Plaster blocks were more effective than mud blocks immediately after the removal of treated papers but

TABLE XXII.

Toxicity of deposits of 10–20 micron gamma-BHC crystals at a dosage of 25 mg./sq. ft. on filter papers which are in turn placed upon different surfaces.

Surface to which papers are applied	No. of days for which applied	Mean percentage kill in 24 hours after exposure of (minutes)							
		0·25	0·5	7	2	4	8	16	32
Glass ...	1	100							
	2	100							
	3	100							
Plaster...	1	100							
	2	70	90	100					
	3	84	95	100					
Mud ...	1	100							
	2	0	20	28					
	3						15	35	95

TABLE XXIII.

Toxicity of surfaces to which the filter papers, sprayed with gamma-BHC crystals as in Table XXII, had been applied for varying periods.

Surface	No. of days for which filter paper applied	No. of days after removal of paper	Mean percentage kill in 24 hours after exposure of (minutes)						
			1	2	4	8	16	32	64
Plaster	1	0	0	38	75	100			
		1			0	25	80	100	
		7					0	5	45
		14					0	0	24
Mud...	1	0		0	15	33	79	100	
		1			0	20	40	95	
		7					0	20	70
		14					0	20	55
Plaster	2	0	15	57	90				
		1			25	45	85	100	
		6					5	50	100
		13					0	10	55
Mud...	2	0		0	19	40	80		
		1			0	20	50	100	
		6					10	50	95
		13					0	40	85
Plaster	3	0	25	60	90				
		5				10	52	95	
		12					0	24	65
Mud...	3	0		0	25	60	90		
		5					10	55	100
		12					5	40	95

subsequent loss in effectiveness was greater with plaster than with mud, as shown in Table XXIII.

These results show, that sorption by mud and plaster blocks of gamma-BHC from treated filter papers occurs in the vapour phase, that sorption by mud is much more rapid than that by plaster, and that desorption occurs more rapidly from plaster than from mud.

Effect of humidity.

It was found that the rate of sorption was affected by the humidity of the atmosphere. Mud and plaster blocks were kept at 78°F. in desiccators over sulphuric acid /water mixtures after treatment with 10–20 micron crystals of DDT and gamma-BHC at a dosage of 25 mg. per sq. ft. It will be seen from the results given in Tables XXIV and XXV that the rate of disappearance of surface deposits increased as the relative humidity of the atmosphere decreased. This may be due to competition between water vapour and insecticide vapour for the internal surfaces of the pores of the mud. This was evident in one test when there was a greater persistence of gamma-BHC on the mud blocks pre-conditioned for four hours in an atmosphere saturated with water vapour than on mud blocks which were sprayed immediately before being placed in the same desiccator.

Another possible reason may be that sorbed and condensed water may reduce the effective diameters of the capillaries and thus reduce the diffusion rate of the insecticide vapour. We are indebted to Dr. A. B. P. Page for this suggestion.

An interesting effect was obtained when the mud blocks kept under anhydrous conditions to give the biological results recorded in Table XXIV were analysed for sorbed DDT. The colour developed in the analytical procedure with these was red indicating that the sorbed DDT had been decomposed to the ethylene derivative, a reaction presumably catalysed by the iron compounds of the mud. A further experiment was performed to confirm this. Mud blocks sprayed with 25 mg. per sq. ft. 10–20 micron DDT crystals were kept at 0, 10 and 20 per cent. R.H. and at 25°C. After one week, when the deposits had disappeared from the surface, analyses were made and showed that 82 per cent. of the sorbed DDT had decomposed in the blocks kept quite dry but none in those kept at 10 and 20 per cent. R.H.

Sorption of DDT by other Soils.

The practical importance of the phenomenon observed on mud from Uganda made it necessary to carry out tests with soils used in the construction of houses in

TABLE XXIV.

Effect of humidity on residual contact toxicity of 10–20 micron DDT crystals at dosage of 25 mg. per sq. ft. on mud blocks kept in desiccators at 78°F.

Relative humidity	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)							
		0·5	1	2	4	8	16	32	64
100% ...	2 days	48	88	100					
	7 days	30	63	93	100				
	14 days			55	78	100			
68% ...	2 days	20	33	75					
	7 days				0	23	60	93	
	14 days						0	0	0
0% ...	2 days	0	0	5					
	7 days						0	0	3

TABLE XXV.

Effect of humidity on residual contact toxicity of 10–20 micron gamma-BHC crystals at a dosage of 25 mg. per sq. ft. on mud and plaster blocks kept at 78°F.

Material treated	Relative humidity	Mean percentage kill in 24 hours after exposure of 15 seconds at different times of treatment					
		1 hour	1 day	2 days	3 days	7 days	14 days
Mud ...	0	100	0		0		
	68	100	0		0		
	100	100	46		0		
	100 (preconditioned for 4 hours)	100	100		5		
Plaster ...	0	100		29		0	0
	68	100		90		65	0
	100	100		95		100	5

other tropical countries. Mud blocks were therefore made from red earths from Uganda, Kenya and Jamaica and from brown earths from Jamaica. A Gault clay from England was also included.

An aqueous suspension of 10–20 micron DDT crystals was sprayed at a dosage of 25 mg. per sq. ft. on to the blocks which were stored at a temperature of 78°F. Sorption of DDT occurred on all blocks, although there were some differences in the times taken for the crystals to disappear from the surfaces. The rate of loss from the surface of the three red earths was very similar, and was greater than that from the Jamaican brown earth and the Gault clay. Results of contact toxicity tests are given in Table XXVI.

Similar results were obtained with a red earth from Nigeria and a brown soil from India.

TABLE XXVI.

Residual contact toxicity of 10–20 micron DDT crystals at dosage of 25 mg. per sq. ft. on mud from different sources ; blocks kept at 78°F.

Source of mud	Age of deposit	Mean percentage kill in 24 hours after exposure of (minutes)									
		0·25	0·5	1	2	4	8	16	32	64	128
Uganda	1 hour ...	35	65	95							
	3 days ...			0	14	55	80	100			
	7 days ...								0	3	25
Kenya	1 hour ...	10	32	60							
	3 days ...			0	0	33	85	100			
	7 days ...								0	24	58
Jamaican (red)	1 hour ...	50	86	100							
	3 days ...			0	0	35	80	100			
	7 days ...								0	0	3
Jamaican (brown)	1 hour ...	30	60	85							
	3 days ...			0	19	60	95	100			
	7 days ...								11	57	98
Gault clay	1 hour ...	30	55	85							
	3 days ...			30	76	100	100				
	7 days ...							0	32	76	100

Discussion.

The most important finding in these experiments from the point of view of the control of malaria vectors by spraying the internal surfaces of houses is the rapid sorption of insecticides by dried mud, especially as the phenomenon occurs on mud blocks made from red earths or lateritic soils used in the construction of houses in many tropical countries (Uganda, Kenya, Jamaica, Nigeria and India). Surface deposits from aqueous suspensions disappear much more rapidly from mud blocks than from any other material tested, and even 10–20 micron particles of DDT, which is usually regarded as a contact insecticide with a long residual effect, are no longer visible after only a few days at 78°F. (25·5°C.).

When DDT and dieldrin crystals are no longer visible on the surface the mud blocks lose their toxicity to mosquitos (*Aëdes aegypti*) exposed to them for long contact periods. On the other hand, blocks treated with the gamma isomer of BHC or aldrin continue to be effective for a considerable time after the disappearance of the crystals. Chemical tests show that with 10–20 micron particles of DDT and gamma-BHC almost the whole of the dosage applied can be recovered from the interior of the block. The residual toxicity after the disappearance of particles of gamma-BHC and aldrin from the surface is due to the fumigant effect from the material inside the block. Desorption of gamma-BHC takes several months for completion as compared with a few hours for the sorption process.

The effect here described gives an explanation for some hitherto rather puzzling results given by Hadaway & Barlow (1949). Recoveries of insecticide from mud blocks sprayed with DDT wettable powders are shown in Table VII of that paper. The percentages recovered from the outer layers are surprisingly low and variable, ranging from 40 to 80 per cent. An obvious reason is now available to explain this as the very rapid loss of surface deposits of DDT from mud was not appreciated and varying periods up to four or five days were allowed to elapse between spraying with the different powders and their analysis.

It is suggested, therefore, that in treatment of mud walls of houses with aqueous suspensions the best residual effects against mosquitos will be obtained with an insecticide such as gamma-BHC which has marked fumigant properties. It is important to determine the part played by fumigation in huts treated with such an insecticide. Ventilation is usually poor ; often there are no windows, and if present these and doors are kept closed at night. Fulton and others (1950) found that houseflies are very susceptible to minute traces of lindane and that 40 per cent. died when suspended in screened cages from 3 p.m. to 9 a.m. from the ceilings of barns 30 days after they were sprayed with a 25 per cent. water dispersible powder at a dosage of 25 mg. lindane per sq. ft.

There are only a few records in the literature of poor results with deposits from DDT wettable powders on materials similar to the dry mud used in these experiments. Fay and others (1948) exposed *Anopheles quadrimaculatus* Say for periods of 60 minutes to deposits of 200 mg. DDT per sq. ft. of a wettable suspension applied to simulated adobe panels made from alluvial clay. Results were disappointing as no residual effectiveness was obtained even though visual evidence indicated an adequate treatment. Sundararaman and Peffly (1949) have compared the residual toxicity of a number of DDT formulations on straw, palm-leaf, and clay-cow-dung panels against houseflies (*Musca domestica* L.) and mosquitos (*A. quadrimaculatus* Say). They have shown that a kerosene solution, an emulsion, and a suspension on straw panels all caused mortalities of 90 to 100 per cent. of the mosquitos for periods ranging from 24 to 32 weeks. On palm panels, however, the solution and emulsion were effective for short periods only, and the suspension continued to kill more than 90 per cent. of both insects for 24 weeks. On clay panels one commercial sample of wettable powder was the best of the treatments but remained effective for only four weeks.

Since the completion of this work two other reports on the rapid loss of toxicity of DDT on mud have been published. Kruse & Konchady (1950) showed that it occurred on clay panels made from soil from a brick yard in Baltimore, U.S.A. Downs, Bordas & Navarro (1951) found a marked difference in the duration of effectiveness of DDT on bricks made from soils from different regions of Mexico, and correlated the persistence of DDT with the iron content of the soil and its activity in catalysing the breakdown of DDT at 130°C. It had been shown in this paper that deposits of gamma-BHC, as well as DDT, rapidly disappear from the surface of mud although this compound is not catalytically decomposed by iron (Riemschneider, 1950, p. 753). Sorption appears, therefore, to be the process responsible for the loss of surface deposits and any decomposition of the insecticide is secondary. As stated by Downs, Bordas and Navarro, however, " the reaction of catalytic decomposition at 130°C. affords a rapid method for foretelling the capacity of a soil for inactivating DDT."

The persistence of an insecticide can be increased by increasing the particle size but this means a loss in effectiveness against mosquitos. DDT particles larger than 40 microns are not very effective against mosquitos and no advantage is to be gained by spraying mud with particles larger than 40 microns. On the other hand, when using a volatile insecticide such as BHC or aldrin which has a fumigant action after the disappearance of surface deposits on mud it is desirable to apply small particles to obtain the maximum initial and ultimate residual effect.

It can be seen from Tables III and V that the relative effectiveness of different particle size ranges of gamma-BHC or aldrin change with time. At first the smaller sizes have a more efficient contact action than the larger but they disappear rapidly by sorption. The blocks retain a fumigant action but this is less effective than contact with the larger particles which still remain on the surface. Ultimately the larger particles also disappear and the blocks sprayed with smaller sizes regain their superiority because, whatever the physical processes affecting the efficiency of sorption may be, the blocks treated with larger particles do not acquire such a pronounced fumigant action as when smaller particles are used. It does not seem possible to deduce more than this from the experiments presented in this paper.

The rate of disappearance of surface deposits is influenced considerably by temperature and the relative humidity of the atmosphere. Volatilisation is much more rapid at 78°F. than at temperatures of 60–70°F. Surface deposits disappeared from mud blocks more rapidly at a low humidity than at a high humidity. Temperatures in houses in tropical countries are often much higher than 78°F. (25·5°C.). Climatic conditions were recorded by Haddow (1942) at Kisumu, Kenya, in a native hut with mud walls and grass roof. It was found that a native hut is a well insulated structure, the temperature range indoors being about half that outdoors. There was an absolute maximum of 33°C., mean maximum of 27°C., absolute minimum of 17°C., and a mean minimum of 20°C. in the hut. The relative humidity ranged from 38 to 79 per cent. on dry days and from 57 to 83 per cent. on wet days.

Deposits from aqueous suspensions of insecticides on non-porous materials such as glass and metal are initially less effective against mosquitos than are similar deposits on porous substances such as mud and plaster. This is because the wetting agent solution is retained on the surface of non-porous materials and when it dries the particles are stuck to the material and are not freely available to insects alighting on or walking on the surface. Visible deposits of all insecticides tested persist on glass, however, for a much longer time than on mud. When the particles of gamma-BHC and aldrin have volatilised from the surface of glass toxicity is completely lost, in contrast to the persistent toxicity on mud after the disappearance of surface deposits. Deposits on a thatch of wheat-stem straw appeared to behave in the same way as those on non-porous materials, but variation in persistence on thatch made from different plants would be expected.

Variation in the duration of residual toxicity on different materials means that emphasis must be placed on the need to study the behaviour and resting habits of different species of mosquitos if the most economical and efficient use is to be made of insecticides. Garnham (1929) at Kisumu, Kenya, found that males of *Anopheles funestus* Giles were more commonly found on the walls and near the floor, while females were commonest on the roof. Gibbins (1933) in Uganda found that *A. gambiae* and *A. funestus* Giles were more commonly found on the upper wall and lower roof. Haddow (1942) divided 318 day-catches into mosquitos caught on the mud wall and those on a Hessian ceiling. Of, 1,168 *A. gambiae* males 97 per cent. were taken on the ceiling, and of 4,380 *A. funestus* males 96 per cent. were taken on the ceiling. Of 4,006 *A. gambiae* females 89 per cent. were taken on the ceiling, and of 8,899 *A. funestus* females 90 per cent. were taken on the ceiling. *Taeniorhynchus* spp. were more commonly found on the walls. Hadaway (1950), in night catches in Uganda, found 79 per cent. of 506 *A. gambiae* and 61 per cent. of 5,006 *Taeniorhynchus* spp. on the thatch roof.

Haddow (1942) classifies *A. gambiae* and *A. funestus* as true house-haunting species which enter both for food and shelter, and *T. africanus* (Theo.) and *T. uniformis* (Theo.) as species which enter huts mainly for feeding purposes. Females of *Taeniorhynchus* spp. are believed to leave the hut soon after biting. It may be significant that treatments of the internal surfaces of native huts are usually less effective against Culicines than Anophelines.

The difference in effectiveness of DDT and BHC wettable powders against *A. gambiae* in houses with mud walls in Africa may be accounted for partly by the ineffectiveness of large DDT particles used in some wettable powders and partly by the rapid sorption of both insecticides into the wall, resulting in the one case (DDT) in a complete loss of toxicity and in the other (BHC) a persistent fumigant effect. Muirhead-Thomson (1950) obtained a lethal action for at least three months after treatment with a " Gammexane " dispersible powder at a dosage of 24 mg. gamma-BHC per sq. ft. in huts with mud walls and palm thatch roof in East Africa. On the other hand, a DDT wettable powder at a dosage of 400 mg. DDT per sq. ft. was very much less effective, and large numbers of mosquitos escaped from the hut unharmed. Bertram (1950) obtained similar results with *A. minimus* Theo. in Assam, also in huts with mud walls. Davidson (1950), in the Belgian Congo, sprayed houses with walls of mud blocks and roofs of various types with Gammexane deposits at the rate of 10 mg. of the gamma isomer per sq. ft. Deposits appeared to retain their toxicity against *A. moucheti* Evans over a period of three months. Results obtained by Wharton and Reid (1950) in Malaya agree with Muirhead-Thomson's in showing the great efficiency of BHC, but differ in showing DDT to be lethal to *A. maculatus*, whereas it was relatively ineffective against *A. gambiae*. The huts were constructed of palm thatch on a wooden framework, and were completely lined with a wrapping paper called " Sisalkraft " which formed the ceiling as well as the walls (Wharton, 1951). DDT deposits would remain effective for a very much longer time on this material than on mud.

The relative residual effects of the four insecticides have been determined under identical conditions of particle size and availability. The length of time during which the solid material remains and acts as a contact insecticide is approximately proportional to its vapour pressure. Figures given in the literature by different workers for the very low pressures of these substances vary a great deal, the variations being of the order of $10–10^2$ at room temperature. It is difficult, therefore, to use the figures given in a discussion on persistence, particularly as the relative accommodation coefficients are not known (see Kuhn & Massini, 1949, for DDT). It is, however, of interest to compare values for different insecticides given by the same author. Apparently only J. Hyman & Co. (unpublished) have measured the actual evaporation rates of all four substances by the same technique and apparatus. They find that in order of persistence at room temperature they may be arranged thus : DDT> dieldrin>gamma-BHC>aldrin. This agrees with the results presented in this paper.

Balson (1947) gives extrapolated values of $9{\cdot}4\times10^{-6}$ and $1{\cdot}5\times10^{-7}$ mm. Hg. at 20°C. for gamma-BHC and DDT respectively. Thus gamma-BHC has a vapour pressure about 60 times that of DDT and this is roughly the ratio of their persistences on mud at 25°C. The ratio of the persistence of gamma-BHC as solid particles on plaster and on mud at 25°C. is about 40. Therefore, as a very rough approximation DDT should remain on plaster at 25°C. for about 7 months. This seems not unreasonable as figures given by Hadaway & Barlow (1951) show no reduction in kill after 21 weeks. Further, the residual life of gamma-BHC particles is longer on non-absorbent surfaces than on plaster and, if DDT behaves in the same way, its life would be comparable with that usually accepted.

Summary.

Factors affecting the persistence of deposits from aqueous suspensions of insecticides have been studied.

There is an inverse relationship between particle size of insecticides and the initial contact toxicity to mosquitos. The influence of particle size on effectiveness decreases as the intrinsic toxicity of the insecticide increases. The compounds investigated can be arranged in order of immediate contact toxicity to mosquitos (*Aëdes aegypti*): dieldrin⩾gamma-BHC>aldrin>DDT.

There is a similar initial inverse relationship between particle size and fumigant effect because of the increase in surface area with decrease in size. The compounds can be arranged in order of fumigant effect on mosquitos :—

Gamma-BHC>aldrin>dieldrin>DDT.

These compounds are not repellent to mosquitos if direct contact is prevented.

The larger the particle the longer it persists. For any given particle size, compounds can be arranged in order of persistence :—

DDT>dieldrin>gamma-BHC>aldrin.

The persistence of particles of these insecticides is influenced considerably by the type of material to which they are applied.

The most striking results are obtained on mud blocks made from red earths or lateritic soils used in the construction of walls of houses in the tropics. Particles of all four insecticides rapidly disappear from the surface, and when surface deposits are no longer visible toxicity is completely lost on DDT- and dieldrin-treated blocks, but persists at a reduced level for many weeks on gamma-BHC and aldrin-treated blocks. Almost the whole of the dosage of 10–20 micron crystals of DDT and gamma-BHC can be recovered from the interior of the blocks. There is ample evidence to show that the residual toxicity of blocks treated with gamma-BHC or aldrin is due to the fumigant effect from the material inside the blocks.

The rate of disappearance of particles from the surface of mud blocks decreases as the relative humidity of the atmosphere increases.

Commercial formulations behave on the different materials in the same way as the pure crystals.

The practical importance of the results is discussed.

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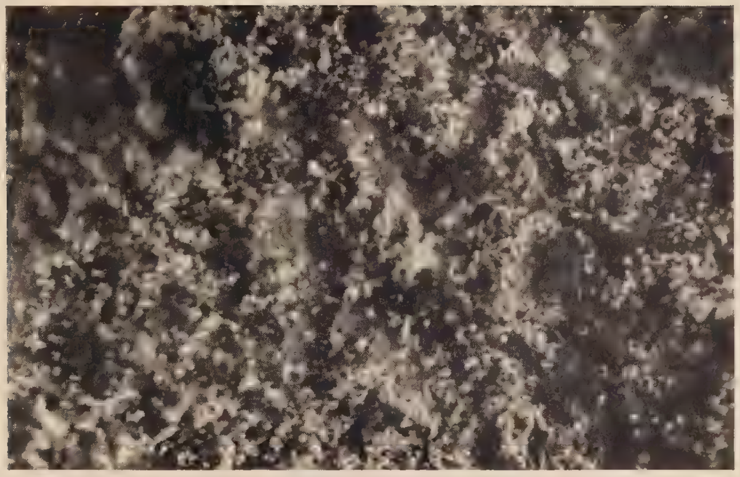
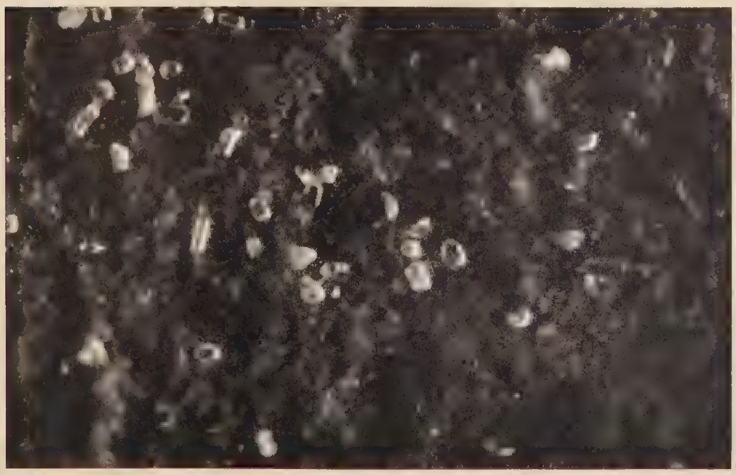


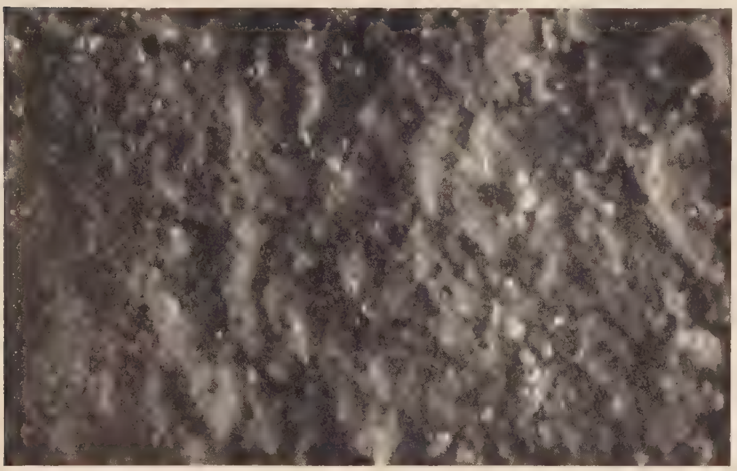
Surface of mud block sprayed with 0-10 micron DDT crystals, one hour after spraying.

Surface of mud block sprayed with 10-20 micron DDT crystals, one hour after spraying.



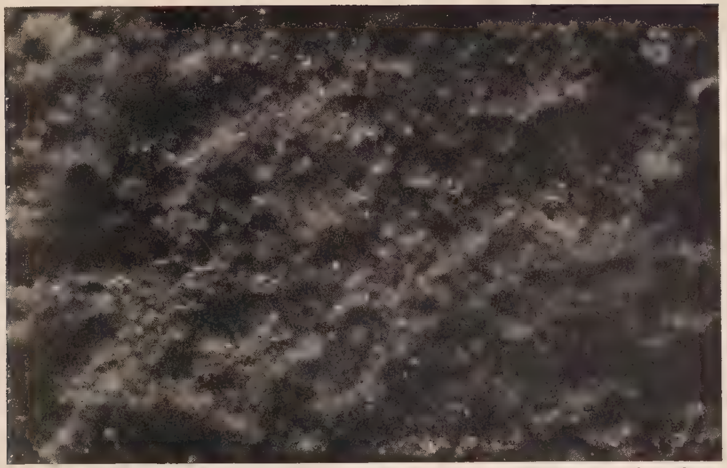
Surface of mud block sprayed with 20-40 micron DDT crystals, one hour after spraying.

Surface of mud block sprayed with 0-10 micron DDT crystals, after two days at 78°F.

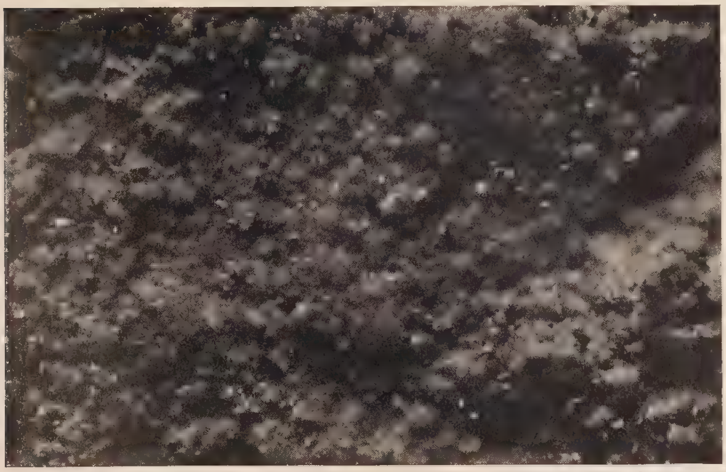


Surface of mud block sprayed with 10-20 micron DDT crystals, after two days at 78°F.

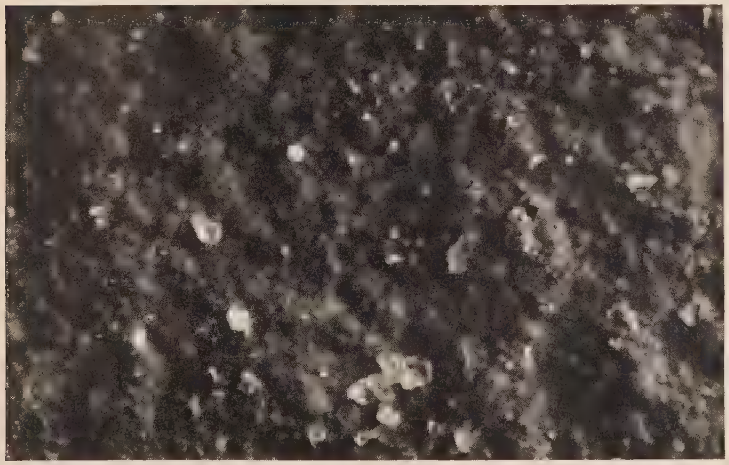
Surface of mud block sprayed with 20-40 micron DDT crystals, after two days at 78°F.



Surface of mud block sprayed with 0-10 micron DDT crystals, after seven days at 78°F.



Surface of mud block sprayed with 10-20 micron DDT crystals, after seven days at 78°F.



Surface of mud block sprayed with 20-40 micron DDT crystals, after seven days at 78°F.

THE SPRAYING OF BAGS OF COCOA BEANS WITH A MACRODOSAGE OF DDT AGAINST *EPHESTIA* AND *TRIBOLIUM*.

By K. G. Smith.

Entomologist, West African Pest Infestation Survey, Lagos.

Cocoa may be stored in Nigeria for several months prior to export during which time it is liable to attack by a number of insect pests, in particular by *Ephestia cautella* (Wlk.) A slight attack by this insect is sufficient to result in down grading and subsequent financial loss. The experiment described below was part of an investigation to determine the best method of preventing such attack. It was thought possible that an application of a heavy dosage of DDT in water suspension to the outside of a stack of bagged cocoa beans would give sufficient protection and the efficiency of this in practice was therefore tested.

The site of the experiment was one of the survey's sheds at Apapa, a small galvanised roofed concrete structure 20 ft. long by 10 ft. wide by 15 ft. high which, having a wooden ceiling, gave fairly constant conditions during the period of observation.

The cocoa treated consisted of two bags of Grade II. The DDT used was a 20 per cent. wettable powder applied by means of an " Eclipse " stirrup type spray pump.

Method.

In order to ensure that it was initially free from active infestation, the cocoa was fumigated with methyl bromide after which it was thoroughly inspected to make sure that no insects had survived. The bags were then placed on the floor of the shed and all their visible surfaces and the surrounding floor sprayed with a 5 per cent. suspension of DDT wettable powder in water. After drying, the fabric of the bags and in particular the protruding fibres, showed a thick white deposit of the insecticide. An analysis by extraction of a section cut from the sack at the termination of the experiment revealed that 956 mg./sq. ft. of DDT was present.

At this stage a small quantity of groundnuts heavily infested with *E. cautella* and *Tribolium castaneum* (Hbst.) was introduced into the shed, being placed as far away as possible from the cocoa and surrounded by a barrier of a " stick tite " material to prevent the migration of larvae from one to the other. In order to follow the population fluctuations, it was necessary to determine the numbers of adult moths bred on the cocoa compared with those introduced. The method employed took advantage of the preference shown by *E. cautella*, noted by Golding (1941), of resting on thin structures such as string and sticks rather than on the flat surfaces of walls and sacks. String was stretched across the store about six feet from the floor and on this a high proportion of the moths (found to be constant when checked over a long period in another store) would be found at rest each morning and could readily be counted.

By following the trend in the numbers it was decided that by the 19th day the majority of the moths from the groundnuts had emerged so what remained were removed. Thereafter all the increase in numbers of moths observed had developed on the cocoa.

Results.

Soon after removal of the groundnuts, *Ephestia* larvae were apparent on the surface of the cocoa sacks, but instead of making for the ears and stitching to pupate, the large majority spun up having moved only a short distance from where they had emerged. As their numbers increased the bag surface rapidly became matted with silk and covered with pupae, a condition that may have been brought about by some slight effect of the DDT. The insecticide was apparently not seriously toxic as all but a very few individuals which might have been expected to have died from natural causes, emerged as adults. What was surprising was the low mortality during emergence, even though the majority of moths had to force their way through DDT covered fibres.

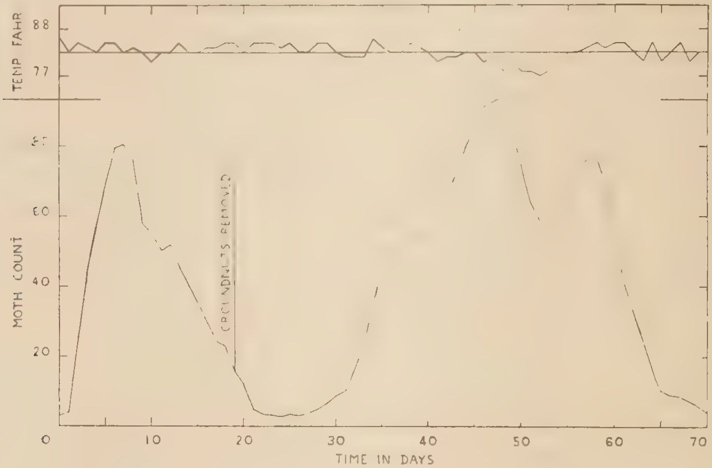


Fig. 1.—Daily fluctuations in temperature and moth count.

The results obtained from the daily counts are shown graphically in fig. 1. A calculation of the number of moth days before the 25th with those to the 70th day shows a relative increase of 1 : 2⅓. It is fairly safe to assume that the average life of the moth is constant throughout the experiment, as there were only slight fluctuations in external conditions. The increase, therefore, must be directly proportional to the increase in the population. Considering that quite a number of larvae of the second generation must have been removed with the groundnuts this represents a very considerable increase which cannot have been greatly affected by the insecticidal treatment. It is obvious that, even with such a heavy dosage, cocoa is far from adequately protected against *E. cautella*.

On the other hand it was apparent that *T. castaneum*, which had attempted to infest the cocoa, had been killed on the surface of the bags as no live adults or larvae were recovered when the beans were finally sieved.

Summary.

The surfaces of bags containing fumigated cocoa were sprayed with the macrodosage of 956 mg./sq. ft. DDT applied as a 5 per cent. suspension of wettable powder in water.

After exposure to an infestation of *Ephestia cautella* and *Tribolium castaneum*, no appreciable effect was obtained in preventing an attack by *E. cautella*, though

the larvae appeared to choose unusual pupation sites on the surface of the bags. *T. castaneum* were rapidly affected and prevented from entering into the sacks.

Acknowledgement.

The author wishes to express his thanks to Mr. H. M. B. Somade, chemist to the West African Infestation Survey, for his help and for carrying out the chemical estimation.

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ON A BRUCHID SEED-BORER IN *ACACIA ARABICA.*

By F. G. G. Peake, M.A., M.Sc.

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The collection of garad (pods of *Acacia arabica* Willd.) for tanning is an ancient industry in the Sudan. *Acacia arabica* is known as sunt in this country and grows naturally along the banks of the Blue Nile where it regenerates freely in the flood-basins. Many of these annually flooded basins, each embraced by a bend of the river, are artificially sown with the tree and protected from grazing ; in due course these form small even-aged crops of timber. The ripe, fallen pods are collected in April and May by the old women of the district who still exercise this privilege even in those areas set aside as forest reserves. These pods are sold to merchants and the seed is dehusked, the primary product being the husk which is used for tanning. The seed is then sold to the Forests Department for sowing, but before sowing it must be treated with strong sulphuric acid to soften the seed-coat and then it must be rinsed in water. Finally, and immediately before sowing, it is soaked in water for 24 hours. This seed is always found to be very largely infertile, most of the kernels having been eaten out by an insect, which has been identified as *Bruchus baudoni* (Caillol), which leaves a round hole in each as a sign of its departure. The infested seed, as it appears in the kernel and also in the pod, is shown in fig. 1.

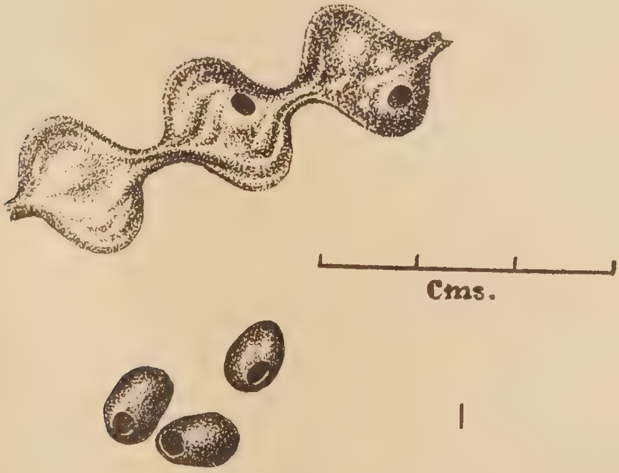


Fig. 1.—Sunt pod and seed, showing exit holes of *Bruchus baudoni.*

Description of the Bruchid.

The beetle when flexed and extended is shown in figs. 7 and 8, respectively. When viewed through a hand-lens, it is seen to have a tortoiseshell-like coloration of black, brown and white scales arranged in adjacent rectangular patches. It is an easily recognised little beetle ; globular, sturdy and abruptly truncated posteriorly in the manner of Bruchids. The size of this beetle is extremely variable and not to be used too readily as a diagnostic feature. Individuals of 4 mm. in length make a good average and the variation is from 3 mm. in small males to 5 mm. in large females. One beetle may, therefore, in volume or weight, be easily twice as big as another. It is an active creature, running and flying briskly and it is strongly attracted to light. Curiously enough, this insect is also occasionally found infesting lubia (*Dolichos lablab*) which commonly grows in the vicinity of sunt trees and which harbours a number of other Bruchids as well. Only one other host-plant has been noted and this from a single record in 1923 (H. B. Johnston) of the insect emerging from the seed of *Abutilon* sp.

Bruchus baudoni is the common Bruchid of *Acacia arabica*. On the other hand, although not so far noted by the writer, there are instances over the past 30 years of other and more polyphagous Bruchids infesting the same seed. At the same time, the decided coloration of *B. baudoni*, together with its great prevalence in sunt seed, makes its confusion with other species unlikely. The other Bruchids recorded in sunt are :—

B. centromaculatus Allard
Normally in *Dichrostachys nutans*, *Acacia spirocarpa* and *A. verugera* ; recorded in *A. arabica*, 1930, 1941.

B. quadrimaculatus F.
In leguminous seeds generally ; recorded in *Acacia arabica*, 1924, 1928.

B. submaculatus Fhs.
Normally on *Albizzia* sp., *Combretum* sp., and *Acacia senegal* ; recorded on *A. arabica*, 1929.

B. theobromae L.
Recorded on *Acacia arabica*, 1944.

B. albonotatus (Pic)
On *Gossypium* and *Acacia tortilis* and recorded on *A. arabica* occasionally.

B. albosparsus Fhs.
On *Helianthus*, *Gossypium*, *Hibiscus*, *Acacia senegal* and on *A. arabica*, 1929.

B. analis F. (*B. maculatus* F.)
On *Vicia faba*, *Dolichos lablab*, *Lens esculenta* and *Cicer arietinum* and *Acacia arabica*, 1944.

B. bedfordi Pic
Recorded on *Acacia arabica*, 1938.

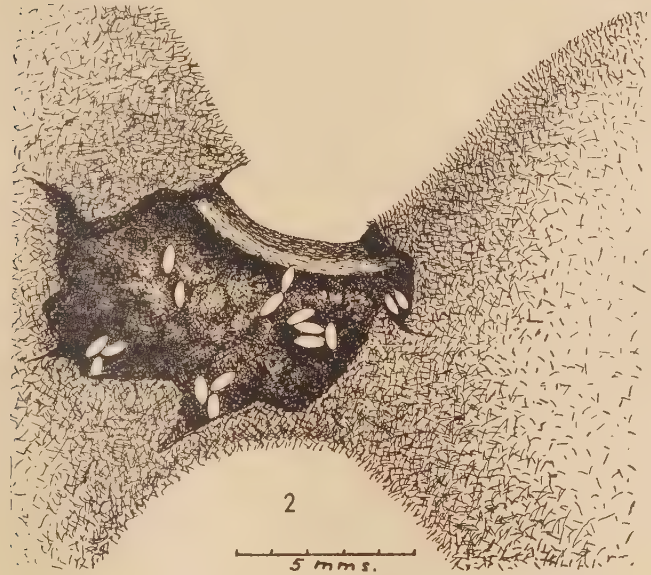
Pachymerus cassiae (Gylh.)
Normally on *Cassia*, *Prosopis*, *Terminalia*, *Cajanus* and occasionally on *Acacia arabica*.

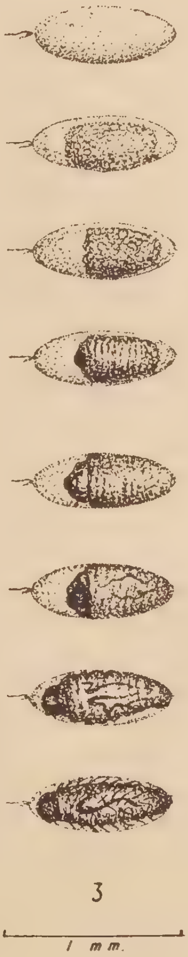
Pachymerus longus Pic
On *Acacia albida* and occasionally on *A. arabica*.

Pachymerus pallidus (Ol.)
Pest of Senna pods ; also on *Medicago* sp., *Terminalia*, *Acacia verek*, *A. albida*, and recorded on *A. arabica*, 1931.

Life-history.

Coition takes place as soon as the beetles emerge from the sunt pods and within 48 hours they return for oviposition. Both males and females are very short lived and commonly die within four days. They could be persuaded to take water and also sugar-water but seven days was almost invariably the maximum longevity in both sexes. The freshly laid eggs are 0·8 mm. in length, elliptical in outline, translucent, and faintly granular on the surface. When the beetles are presented with the hard, husked seed, these eggs are deposited anywhere, either on the seed itself or all over the container. The beetle does not discriminate between good seed and seed already empty of a kernel. The eggs are extremely fragile, the slightest touch flattening them out completely against the surface to which they are lightly gummed by the parent beetle. It seems likely that any disturbance in a sack of husked seed would destroy the majority in a very short time. With the unhusked seed in the pod, however, the state of affairs is very different. Eggs are then rarely laid in an exposed position but wholly in the broken portions of a pod where crevices and natural excavations provide some protection. The natural dehiscence found along the border of a sunt pod does not appear to be sufficiently wide to allow of oviposition





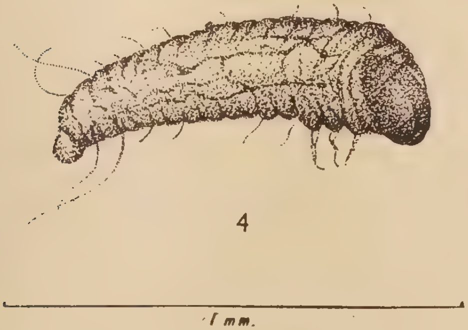


Fig. 2.—A typical oviposition site in the broken shell of a pod.

Fig. 3.—Development of the egg from the first to eighth day.

Fig. 4.—Young larva in the walking stage before entering the seed. Note the thoracic legs.

although an occasional egg may be found therein. Ten or twenty eggs and more, however, may often be found in the broken part of a pod or in any vantage point affording shelter. Even dead and headless beetles found amongst the pods may be made use of as receptacles for eggs. A typical egg-site on the broken surface of a pod is shown in fig. 2 while fig. 3 illustrates the egg itself in embryonic development from the first to the eighth day.

The young larva, fig. 4, which hatches out on the 9th or 10th day, is extremely active and regularly makes a peregrination over and among innumerable pods before settling down to bore. The first-instar larva is large in the head and thorax, tapering to a small and downward-curved extremity which has the power of prehension so that this minute grub may often be seen standing vertically on end, swaying in the manner of a caterpillar. It will be seen from fig. 4 that it is well

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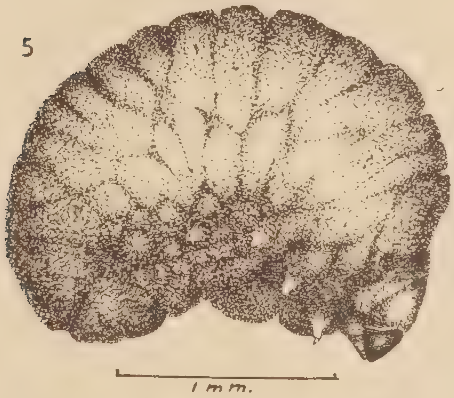

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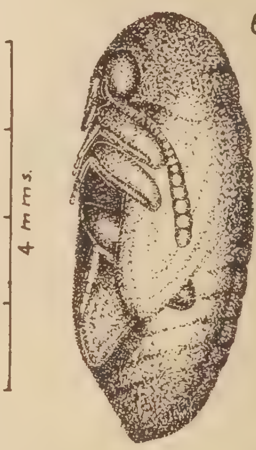

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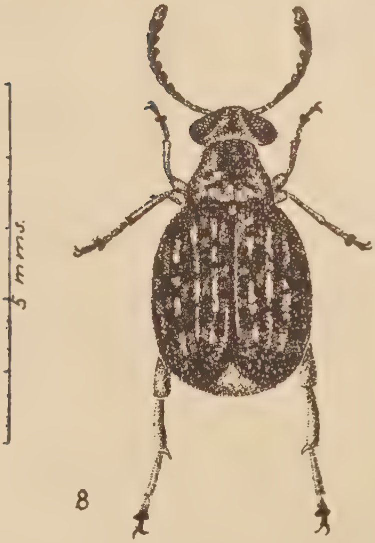

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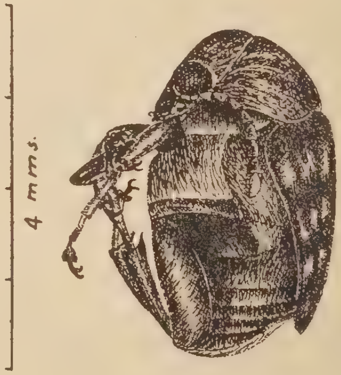

Fig. 5.—*Bruchus baudoni.*—Half-grown larva from the seed-kernel, showing reduced thoracic legs.

Fig. 6.—Pupa. Fig. 7.—Adult, flexed. Fig. 8.—Adult, extended.

furnished with long hairs which are directed outwards and backwards and that the two posterior pairs are exceptionally long. Its length, 0·8 mm., equals that of the egg from which it has escaped by a circular opening in the end.

It is particularly noteworthy that this larva has, at this stage, well-developed thoracic legs and makes this long perambulation before settling down. Unlike other Bruchids which bore directly into the seed through the floor of the attached egg, the larva of *Bruchus baudoni* exhibits this vulnerable period in its life-history, a period when, in treated seed, it would encounter an insecticidal deposit.

From the moment the young larva enters the seed, it is not easy to follow its development, acacia seed being extremely hard and difficult of dissection. Breaking open infested seed at intervals does, however, show that after entry, the larva becomes fat and grub-like and that the thoracic legs become reduced and barely visible. Fig. 5 shows the rotund appearance of this larva. In dissecting this seed, infested material may first be recognised by the original entry hole of the newly hatched larva. This hole is extremely small, only 0·2 mm. in diameter, but may always be detected somewhere on the seed-coat.

The pupa is illustrated in fig. 6. The total life-history occupies from five to six weeks, the average being 39 days. This is with caged seed under natural open-air conditions.

Experiments on old and new Pods.

A small sack of the sorted, natural pods, exactly as collected off the forest floor, was used to make several counts as a means of getting an idea of the percentage infestation. The sack-full was, in fact, a sample of the garad as it goes to the merchants and its contents represented a random collection from the forest. It had been in store about 18 months. From the number of exit holes in the pods, the infestation was found to be 61 per cent. As there is only one seed in each segment of a pod, and as each segment in the sunt pod is narrowly constricted from its fellow, these exit-holes represent the number of seeds which have been infested. It follows that when the merchant has removed the husk and returned the seed to the Forests Department, out of every ten sacks received, only four are fertile. It also means that 60 per cent. of the sulphuric acid treatment is wasted unless, by testing the seed by floating, only the 40 per cent. good seed is treated, and even this would not be really a very accurate process. Now as the pods, such as those in the sample sack, may remain stored from one to two years before being dehusked, and as the sacks are found, when opened, to contain the live beetles, it has been supposed, very naturally, that the insect was essentially a pest of stored products. As such, it might be easy enough to control with BHC dust sprinkled in with the pods in each sack. But before making this recommendation it was thought advisable to carry out some preliminary observations on the habits of the insect. To this end, insectaries were prepared for breeding the beetles, and sunt pods were put therein. These were taken : (*a*) from old stock stored in sacks, (*b*) from the forest, immediately the pods fell from the trees, (*c*) from the trees themselves before the pods had fallen. No time was lost in transferring the fresh pods to the insectary. Surprisingly enough exit-holes of the beetle were found to be already present in as many as eight per cent. of the freshly fallen pods and even occasionally in the green pods from the trees themselves.

All the above three categories of pods were caged and observed. Category " c " (covering the earliest stages of infestation) gave the most complete results and those for the five months, April to August 1951, are shown graphically in fig. 9, the daily emergence of the beetles from the fresh seed being correlated with mean temperature and mean humidity. For the sake of space, only this active five months of the year is shown in the graph. The pods were actually caged on 4th March and the observation extended until the time of writing, in early December. No further activity is anticipated before the onset of the rainy season in May 1952, none that is, beyond the regular small emergence of beetles as noted at either end of the graph. Presumably, these beetles of the dry season oviposit on the old pods on the forest floor as they are seen to do on dry and very old pods in the insectaries.

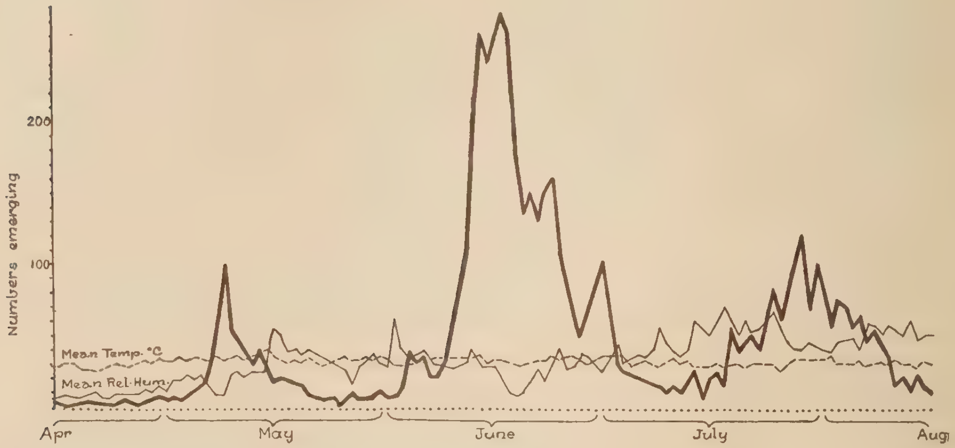

Fig. 9.—Graph showing relation between temperature, humidity and the daily emergence of *B. baudoni* over five months. The same units are used for temperature, humidity and insect numbers but the humidity curve has been displaced upwards.

Passing over for the moment the question of temperature and humidity, it should first of all to be noted that beetles emerged from fresh green pods after these had been caged. Therefore eggs must have been laid on these fresh pods whilst still on the tree. This means that damage caused by the pest cannot be completely eliminated by treatment of the stored seed ; the insect will constantly be coming in from the forest however fresh the seed may be when collected. This percentage of damaged seed is inevitable apart, that is, from possible biological control in the forest. Throughout the same five months, the old, stored seed produced a regular small number of beetles day by day and its infestation eventually exceeded 80 per cent.

In all these insectary cages the newly emerged beetles, which flew up out of the seed spread over the floor, were removed daily and counted. As flight always appears to precede mating and as the beetles are strongly phototropic, this daily number caught and removed from the cages fairly represents the daily emergence, a few escaping to produce the next generation.

Such were the conditions in the insectary with green pods collected off the trees early in March. Under natural conditions, the pods would have remained on the tree for a short time, to have fallen later and completed their desiccation on the forest floor. Enquiries put to Forest Officers and the older inhabitants of Blue Nile Province led to a fairly unanimous conclusion that *Acacia arabica* flowers in the late rains (that is, October to November) and that green pods are found on the tree from late December until they fall in March and April. The seed then remains on the forest floor without germinating for five years or more. From this it will be seen that in the natural forest there is, at any time, a quantity of dry pods of various ages at hand for oviposition. For the first four months of the year there is also a selection of green pods on the trees. At the same time it is difficult to correlate the 39-day rhythm of wet-season generations (fig. 9) with the unfluctuating small emergences throughout the long dry period, and no explanation is attempted here. It is, however, possible that by using large insectaries with many hundredweights of pods, the more closely ordinated graph might indicate perceptible fluctuations. At all events it appears that there is no complete diapause. It will be seen from the graph that the temperature remained high right through the period of the experiment and, on the face of it, one would say that humidity was the activating factor.

Suggestions for Control.

Spraying or dusting of mature sunt forest to prevent initial attack in the green pod is clearly impracticable and this original infestation must be taken as a necessary evil. The pods, by the time they are collected off the forest floor, will already be infested to some extent and beetles from 8 per cent. of the seed will have already flown. In the sacks, when stacked for several months, the pods will become reinfested to the extent of 60 per cent. of the seed and if stored long enough, to 80 per cent. It should be possible to prevent this reinfestation by means of an insecticide, since it has been shown in these experiments that the beetle has a very vulnerable stage in its life-history, a stage in which it is unprotected and moves freely amongst the pods. This supports the proposal to use a contact insecticide, which would leave a persistent deposit on the pods, rather than the use of a fumigant. As a test of the costs and effectiveness of insecticidal treatment, the collecting stations at Suki and Singa have been supplied with BHC dust (Agrocide 3) to mix in the proportion of 1 per cent. by volume with the pods as they come in from the forest. Untreated pods have also been put aside as a control. Samples of these treated and untreated pods will be examined at intervals over the period for which they are normally kept in store.

The question of biological control of *Bruchus baudoni* is being considered. It is a remarkable thing that other *Acacia* species in the Sudan, *A. albida*, *A. mellifera*, *A. seyal* and no doubt many more, support both Bruchids and their parasites, whereas sunt (*A. arabica*) has never shown any parasitism among the many thousands of beetles bred in the insectaries.

Sunt appears to be botanically identical with the babul of India and this led to the search for a parasite there, but in India *B. baudoni* itself has not been recorded on the tree. Again it was thought possible that the Lablab Bean of India (*Dolichos lablab*), having been brought to the Sudan many years ago, might furnish the beetle and its parasite, but investigations have yielded negative results.

The fact that the *Acacia arabica* of the Sudan is separated by such vast distances from the same species in east, central and west Africa, and that *B. baudoni* is known to exist in these countries, may yet lead to the discovery of a parasite. Investigation is proceeding.

Summary.

Bruchus baudoni (Caillol) infests the seed of *Acacia arabica* in the Sudan and renders it largely infertile. Attack is not only in stored seed but also in the green pods before these have fallen from the trees. The life-history was studied and the newly hatched larva found to move freely about amongst the seed before boring. As this vulnerable stage occurred only once every six weeks with each new generation, a contact insecticide rather than a fumigant would be more likely to give satisfactory control. Parasites were found of the Bruchids of other *Acacia* species but not on *B. baudoni*. The search for a parasite is being extended to east, central and west Africa as the *Acacia arabica* of these countries is widely separated from that of the Sudan.

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PARASITES OF THE MOTH-BORERS OF SUGAR-CANE IN MAURITIUS.

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and

Claude M. Courtois,
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There are three moth-borers of sugar-cane in Mauritius. These are : (*a*) the spotted borer, *Proceras sacchariphagus* Bojer (Crambidae), (*b*) the pink borer, *Sesamia vuteria* (Stoll) (Agrotidae) and (*c*) the white borer, *Olethreutes schistaceana* (Sn.) (Olethreutidae). The bionomics of these borers have been described by Moutia (1934), and the bibliography in a paper by Moutia and Mamet (1945) may be referred to for further information about these important pests.

The parasites of the three borers were studied by d'Emmerez de Charmoy (1917), and the present paper recounts an investigation which was undertaken to extend and verify his work and, by doing so, to set a basis for future attempts to control these moths by biological methods.

The names used in this paper for the three borers of sugar-cane and for other Lepidoptera that are mentioned are in most cases those used by the authors of the papers cited as references. Although some of the names are not wholly correct or are synonyms, while in other cases there are alternative generic names that are commonly used, the earlier names are retained to avoid the confusion that might otherwise arise when the papers cited are consulted. A list of all such names, followed by their modern equivalents or alternatives, is given below :—

Sesamia vuteria (Stoll)	*Sesamia calamistis* Hamps.
Olethreutes schistaceana (Sn.)	*Argyroploce schistaceana* (Sn.)
Eucosma schistaceana (Sn.)	*Argyroploce schistaceana* (Sn.)
Carpocapsa pomonella (L.)	*Cydia pomonella* (L.)
Diatraea striatalis Sn.	*Proceras sacchariphagus* Boj.
Diatraea venosata (Walk.)	*Proceras venosatus* (Walk.)
Diatraea polychrysa Meyr.	*Proceras polychrysa* (Meyr.)
Diatraea auricilia (Dudgn.)	*Chilotraea auricilia* (Dudgn.)
Chilo infuscatellus Sn.	*Chilotraea infuscatellus* (Sn.)
Chilo simplex (Butl.)	*Chilo suppressalis* (Walk.)
Omphisa illisalis (Walk.)	*Omphisa anastomosalis* (Gn.)

The developmental stages of the parasites were studied from hosts parasitised in the laboratory. Dissections were made either in isotonic sodium chloride solution or in Ringer's solution. For descriptive purposes, material was mounted in de Faure's medium either directly or after treatment with KOH, or was stained in strong Gage's acid fuchsin prior to mounting in Canada balsam.

Egg Parasites.

Platytelenomus sp. (? *hylas* Nixon) (Hym. Scelionidae).

This species was referred to by d'Emmerez de Chamroy (1917) as *Telenomus* sp. and he recorded it as a parasite of *Proceras* and *Sesamia*. In 1921, d'Emmerez de Charmoy and Gébert also recorded it from *Prodenia litura* (F.) ; Van Dine (1929), when listing the Scelionid parasites of sugar-cane moth-borers, considered the insect to be *Prophanurus alecto* Crwf. rather than a species of *Telenomus* and this name was adopted in all publications subsequent to that date.

During this investigation, specimens bred from eggs of *Sesamia vuteria* were submitted to the Commonwealth Institute of Entomology and were kindly identified by Mr. G. E. J. Nixon as *Platytelenomus* ? *hylas* Nixon. That the specimens were of the same species as that studied by d'Emmerez de Charmoy was verified by examination of his original slides. *P. hylas* Nixon was described from specimens parasitising eggs of *Sesamia cretica* (Led.) in the Sudan (Nixon, 1935).

Egg (fig. 1 *a*).

Ovate, white, transparent and provided with a pedicel ; there is no demarcation line between body and pedicel. The yolk material occupies from one-half to one-third the egg body. During incubation the egg becomes almost globular. Overall length 0·14 mm. pedicel 0·07 mm. or less. Greatest width 0·03 mm.

First-stage larva (fig. 1 *b*).

On eclosion the first-stage larva is white, transparent and measures 0·15 mm. in length. The head, thorax and abdomen are distinctly separated, the junction of head and thorax being the clearer. The measurements, taken from a lateral view are : head, 0·06 mm. long, 0·053 mm. wide ; thorax, 0·015 mm. long, 0·023 mm. wide ; abdomen, 0·076 mm. long, 0·067 mm. wide. The head is curved. The mandibles (fig. 1 *b′*) are well developed, broad at their base, curved and pointed. Their total length is about 0·25–0·35 mm. Below the mandibles there is a slight protuberance and also a conspicuous fleshy lobe which may represent the rudiments of the labium.

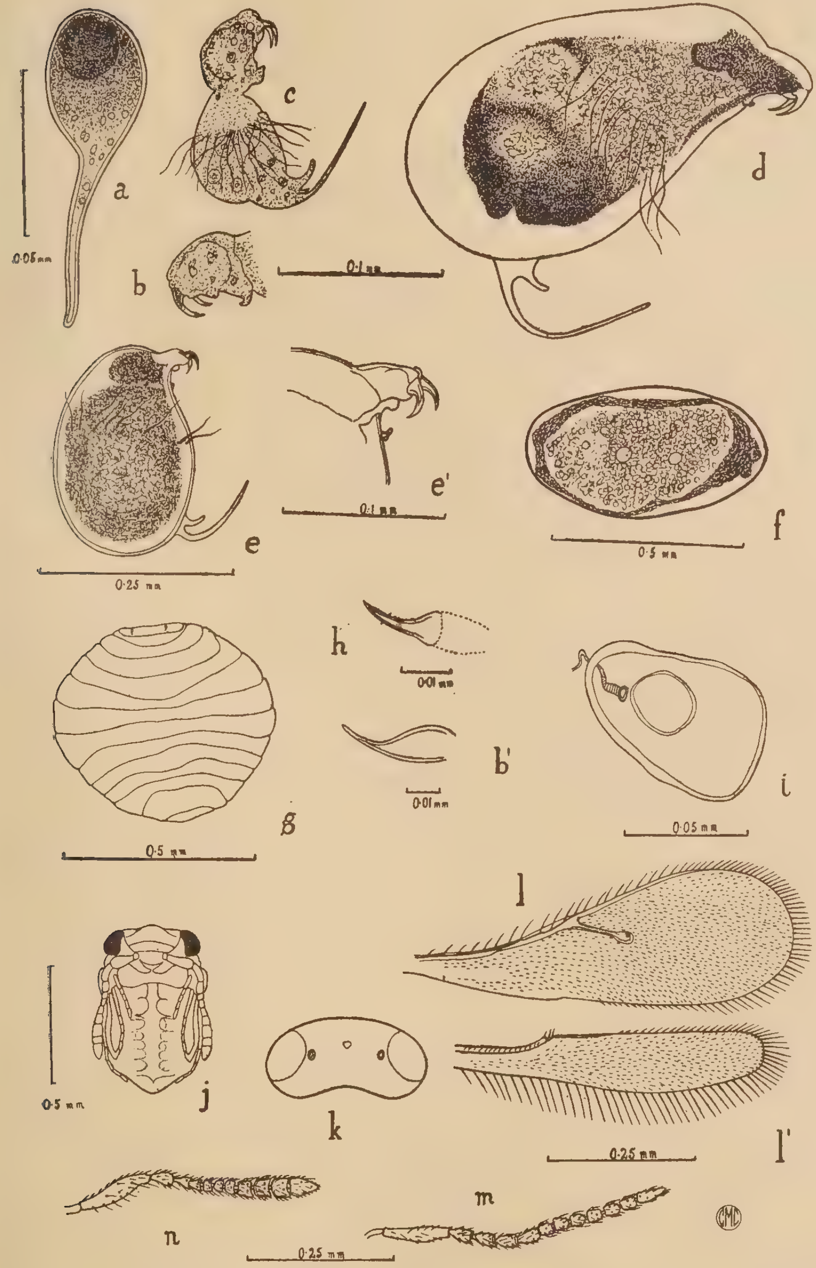
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Fig. 1.—*Platytelenomus* sp. ? *hylas* Nixon : *a*, egg ; *b*, first-stage larva showing division between head and thorax ; *b′*, mandible ; *c*, larva, 48 hours old ; *d*, larva, 96 hours old ; *e*, larva, 120 hours old ; *e′*, head of *e* ; *f*, second-stage larva ; *g*, third-stage larva ; *h*, mandible ; *i*, spiracle with spiracular plate ; *j*, pupa ; *k*, enlarged portion of head ; *l*, forewing ; *l′*, hindwing ; *m*, male antenna ; *n*, female antenna.

The body shows no constriction where the thorax and the abdomen are presumed to meet, but there is a girdle of long, hair-like setae of about equal length, measuring 0·068 mm. approximately. These setae number at least 25. The abdomen bears three unsclerotised ventral outgrowths near its extremity, two of which are small and stout and the third long, sickle-shaped and reaching the region of the head when in movement. The alimentary canal is simple and sac-like. When about two days old (fig. 1 *c*), the fleshy lobe of the labium is more developed, the division between head and thorax is beginning to disappear and a constriction is formed ventrally between thorax and abdomen. The abdomen has increased in size and is more globular. A small fleshy lobe on the extremity of the head is visible. After about four days (fig. 1 *d*), the demarcation between head, thorax and abdomen has disappeared, as has the smallest caudal outgrowth, and the larva is pale-green in colour. Finally, when about five days old (fig. 1 *e*, *e*′), the larva is ovoid in form, pale-yellow to pale-green in colour and the body entirely filled by the gut. When about seven days old, the larva is about to moult, and the remaining caudal outgrowths have disappeared.

Second-stage larva (fig. 1 *f*).

The second-stage larva has a cylindrical body, in the interior of which large granules are visible. The mandibles are difficult to see and appear to be invaginated in the head region. A slight fold of the skin is sometimes apparent and might represent a trace of segmentation. Length 0·57 mm., greatest width 0·32 mm. This stage lasts for about 24 hours. Neither the first nor the second stage has any tracheal system.

Third-stage larva (fig. 1 *g*).

The third-stage larva is almost globular ; the whole body is smooth, dirty-white in colour, without setae and composed of 13 distinct segments excluding the head. In the head region, structures which seem to represent the antennal organs are just apparent ; they consist of small crenate elevations. The mandibles are curved and pointed (fig. 1 *h*). A pair of subcircular swellings occurs near the thoracic segments. The spiracles are associated with a ring-like structure on the body as shown in fig. 1 i. The tracheal system is well developed. The nine pairs of spiracles which are visible are connected with a tracheal trunk on each side, one pair on the mesothorax, one on the metathorax and one on each of the first seven abdominal segments.

When fully grown, the larva measures 0·75 mm. in length and its greatest width is 0·59 mm. The third stage lasts for about eight days. Before the larva passes into the prepupal stage, a meconium is passed.

The prepupal stage is of one to two days' duration. The prepupa is pale-green to dirty-white in colour and is cylindrical. Dimensions : length, 0·81 mm. ; greatest width, 0·60 mm.

Pupa (fig. 1 *j*).

The pupa is whitish ; the eyes and ocelli are reddish-brown and the abdomen almost globular. It measures 0·66–0·69 mm. in length and 0·37–0·43 mm. in width.

Adult.

Reference should be made to the description of *P. hylas* by Nixon (1935), although as mentioned above the insect has not definitely been identified as this species. The head, antennae and wings are shown in fig. 1 *k*–*n*.

Life-history.

Copulation occurs immediately after emergence and lasts for 30 seconds to five minutes. Oviposition follows at once if host eggs are available and is completed in 30 seconds to two minutes. No particular portion of the host egg is chosen for the insertion of the ovipositor and the female does not feed at the puncture it has made. Oviposition will occur only in *Sesamia* eggs that are not more than four days old.

Superparasitism is readily induced in the laboratory and as many as five larvae have been seen in one egg, although only one succeeds in completing development. Very occasionally a single egg yields two adults, but this has only been observed among parasitised eggs collected in the field.

The length of life of the adult is dependent upon food and temperature. Without food, it does not exceed four days in summer and nine in winter. With sugary foods and when allowed to oviposit, a female lives five to seven days in summer (mean temperature 22·8°C.), and an average of 35 days in winter (mean temperature 18·8°C.) with a maximum of 45 days.

The ovaries each consist of four ovarioles, and a newly emerged female contains a total of 12–23 fully developed eggs. The average number of eggs laid by 12 mated females kept separately in 6 × 1-in. tubes with food and an abundant supply of host eggs was 69, the maximum being 81 and the minimum 57. In summer, all the eggs are laid within four days of emergence, about 46 per cent. on the first day, 31 per cent. on the second, 17 per cent. on the third and 6 per cent. on the fourth. With the increased duration of life in winter, half of the eggs are laid on the first day and the remainder at irregular intervals until the 20th day.

The durations of the various stages of the life-cycle in eggs of *Sesamia* are given in Table I. The newly hatched larva shows constant movement which decreases when the second instar is reached. The host egg generally becomes grey or greyish-black on or about the ninth day of parasitism.

TABLE I.

Duration of the various stages of development of *Platytelenomus* sp. ? *hylas* in eggs of *Sesamia vuteria*.

	Dec. to Feb. (days)	March to May (days)	June to July (days)
Egg	1–1½	1—2	2
1st larval stage	5–6	6–8	4
2nd larval stage			2½
3rd larval stage			8½
Prepupal stage	1–1½	1½–2	2
Pupal stage	5–8	13–16	14
Egg to adult	12–17	21½–28	33
Mean Temperature	23·9°C.	21·5°C.	17·9°C.

Sex Ratio and Parthenogenesis.

The numbers of males and females appear to be about equal, for in 1,226 adults obtained from field-collected host eggs and from laboratory breedings, the sex ratio, male to female, was 1 : 1·28. There is however, considerable variation in the ratio with individual batches of field-collected host eggs.

Parthenogenesis occurs readily and the offspring are invariably male. The fecundity of unfertilised females appears unaffected.

Hosts.

Collections of Lepidopterous eggs on various food-plants were made during the winter season with a view to obtaining some information on hosts other than *Sesamia vuteria*. The results of these collections are shown in Table II.

Only one new host, *Autographa chalcytes*, is recorded. This insect is a common pest of tomato plants and is of wide distribution in the island. The parasitised eggs were chiefly obtained on tomato plants near sugar-cane fields and it may be inferred that *A. chalcytes* is an alternative host during the winter when *Sesamia* eggs are very scarce in cane fields.

TABLE II.

Species	Food-plant	No. of eggs collected	Percentage parasitism by *Platytelenomus*
Autographa chalcytes (Esp.)	Tomato	342	2
Proceras sacchariphagus Boj. ...	Sugar-cane	4,500	Nil
Melanitis leda (L.)	Sugar-cane	268	Nil
Achaea trapezoides (Gn.)	Castor Oil	315	Nil
,, ,, ,, ...	*Acalypha*	225	Nil
Heliothis armigera (Hb.)	Tobacco	650	Nil
Prodenia litura (F.)	Tomato and Sugar-cane	220	Nil

The records of *Proceras sacchariphagus* and *Prodenia litura* as hosts (d'Emmerez de Charmoy, 1917 ; d'Emmerez & Gébert, 1921) were not confirmed by these collections. It may be added that the results of laboratory contacts of the parasite with *Proceras* eggs were always negative, while the examination of *Proceras* eggs in previous years (Moutia & Mamet, 1945) also failed to reveal parasitism by this Scelionid.

Natural Parasitism of Sesamia vuteria *(Stoll).*

Monthly collections of *Sesamia* eggs were made to assess the incidence of parasitism throughout the year. *Sesamia* does not lay its eggs directly upon sugar-cane, but upon a variety of graminaceous weeds, and the larvae migrate to neighbouring cane plants when they are partially grown. Collection of eggs in quantity from these grasses is difficult, but oviposition occurs very readily on maize, so that for convenience collections were restricted to this plant. The majority of the eggs so collected were from upland areas where *Sesamia* is always most numerous.

Table III shows the degree of parasitism which occurred in the monthly samples of eggs. The number of host eggs collected each month gives a rough indication of the seasonal incidence of *Sesamia*. The greatest parasitism occurred during the

TABLE III.

Percentage of *Sesamia* eggs parasitised by *Platytelenomus ? hylas* throughout the year.

Months	No. of eggs collected	No. of eggs parasitised	Percentage parasitism
November 1949	315	0	Nil
December ,, ...	320	45	14·0
January 1950	1,809	28	1·5
February ,, ...	840	80	9·0
March ,, ...	516	62	12·0
April ,, ...	200	10	5·0
May ,, ...	135	40	29·6
June ,, ...	178	26	14·6
July ,, ...	123	40	32·5
August ,, ...	184	12	6·5
September ,, ...	342	0	Nil
October ,, ...	240	0	Nil
Total	5,202	343	—

Mean percentage parasitism (from totals above) : 6·5 winter months of May–July when *Sesamia* is scarce, while in January–February when injury to cane by this moth is at its peak, parasitism was low. Of the total of 5,202 eggs (175 batches) which were collected throughout the year, the percentage destroyed by *Platytelenomus* was only 6·5. These figures compare most unfavourably with those given by Bedford (1935) for the parasitism of *S. cretica* in the Sudan, where 99 per cent. parasitism was reported.

Trichogramma sp. (? *australicum* Girault) (Hym., Trichogrammatidae).

This species was submitted for identification to the Commonwealth Institute of Entomology. The material was examined by Mr. G. J. Kerrich, who reported that, having compared it with Girault's description of *australicum*, he was unable to identify it with certainty, because the description was inadequate, but he thought it was *T. australicum* and almost certainly not *T. minutum* Riley.

T. australicum is known as an indigenous species in Australia, where it attacks numerous Lepidoptera among which one of the most important is the codling moth, *Carpocapsa pomonella* (L.) (Allman, 1927). It is also recorded from Java (Girault, 1914 ; van der Goot, 1915) as indigenous. Its hosts in that country are *Diatraea striatalis* Sn., *Chilo infuscatellus* Sn., *Chilo simplex* (Butl.), *Olethreutes schistaceana* (Sn.) and *Scirpophaga innotata* (Walk.). The latter, a pest of rice, is kept in check by this parasite (van der Goot, 1925). In Formosa, it parasitises eggs of *Diatraea striatalis, Chilo infuscatellus* and *Olethreutes schistaceana*, in that order of preference (Takano & Yanagihara, 1939). In Japan, it is recorded by Ishii (1938) as a parasite of *Chilo simplex*. In Ceylon, the Tea Tortrix, *Homona coffearia* (Nietn.) is recorded as another host (Jardine, 1918). The parasite has been introduced from Java to Hawaii to further the control of *Chilo simplex* (Fullaway, 1930). In Madagascar, it is a probable parasite of *Diatraea venosata* (Walk.) and *Sesamia vuteria* (Frappa, 1935). In Mauritius, its recorded hosts are *Proceras sacchariphagus* and *Sesamia vuteria* (d'Emmerez de Charmoy, 1917). In addition, the following hosts have been used for the mass-breeding of it in the laboratory : *Sitotroga cerealella* (Ol.), *Ephestia cautella* (Walk.) and *Corcyra cephalonica* (Staint.) (Takano, 1933 ; Jepson & Moutia, 1939).

Egg (fig. 2 *a*).

Transparent, and elongate or fusiform in shape, with the anterior end slightly pointed and the posterior end smoothly rounded. It can be easily found in the host egg by transmitted light. Before hatching it becomes granular in appearance, pale-yellow in colour and increases considerably in size, sometimes to five or six times that of freshly-laid eggs. Immediately after deposition, the mean length is 0·11 mm. and its greatest width 0·05 mm.

First-stage larva (fig. 2 *b*).

On eclosion is elongate-oblong and is wider posteriorly. Segmentation is entirely lacking. The integument is wrinkled in parts, this being more apparent in a living larva. No cuticular processes or appendages are visible. The mandibles are faintly visible and rudiments of the mouth-opening are discernible. The gut is sac-like, filling three-quarters of the body. The average length is 0·32 mm.

The larva starts feeding as soon as it hatches and shows considerable movement in the egg yolk for the first 24 hours. Sometimes remnants of a hyaline envelope resembling the chorion of the egg remain attached to the posterior extremity of the larva (fig. 2 *c*).

Second-stage larva (fig. 2 *d*).

About two days after hatching the second-stage larva is globular and the mandibles are more apparent and lie parallel to one another ; they are slightly

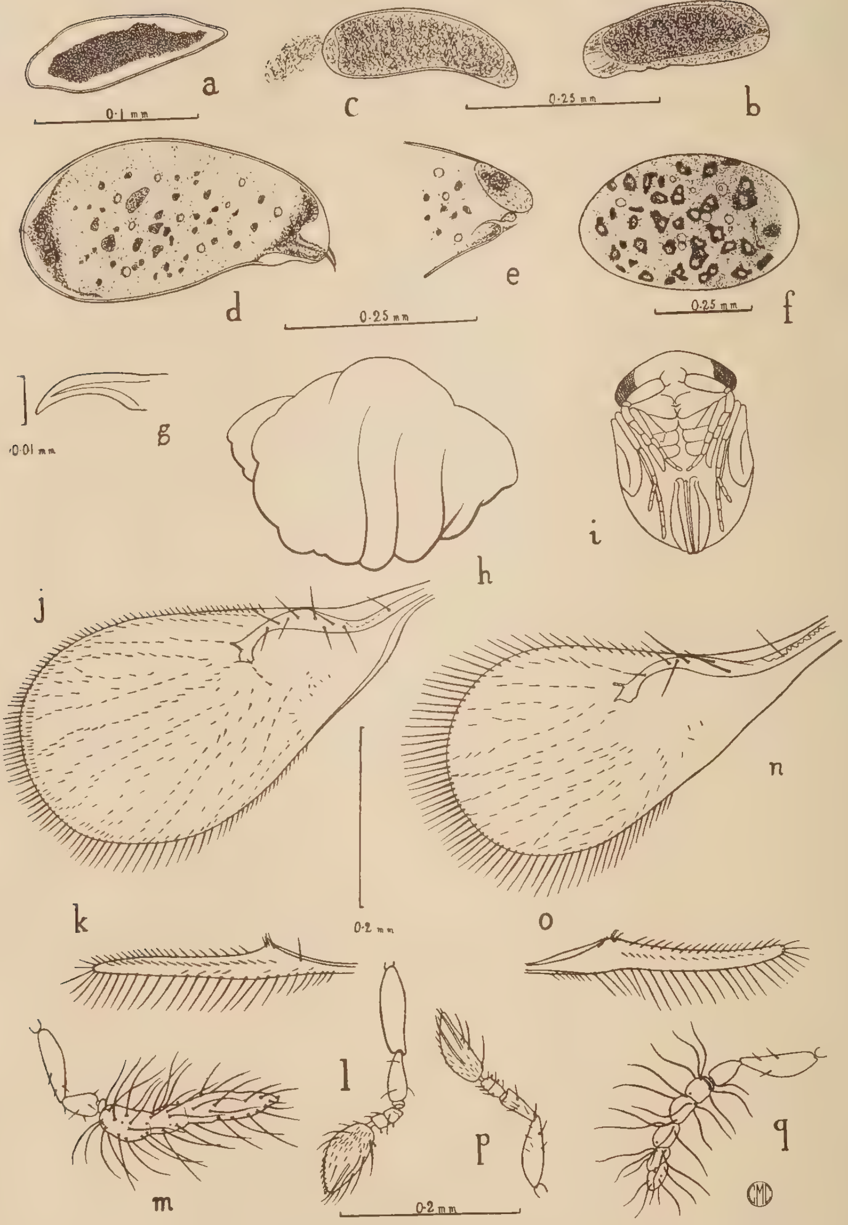
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Fig. 2.—*Trichogramma* sp. ? *australicum* Gir. : *a*, egg ; *b*, newly-hatched larva ; *c*, first-stage larva, 24 hours old with egg envelope attached to it ; *d*, second-stage larva ; *e*, head of second-stage larva showing mouth opening ; *f*, third-stage larva ; *g*, mandible ; *h*, prepupal stage ; *i*, pupa ; *j*, forewing ; *k*, hindwing ; *l*, female antenna ; *m*, male antenna.

Trichogramma sp. : *n*, forewing ; *o*, hindwing ; *p*, female antenna ; *q*, male antenna.

curved and pointed. The gut fills the entire body except for a very small part anteriorly. No wrinkles are apparent in the skin. Its colour is light-yellow and the integument transparent. An opening or mouth-like organ is sometimes visible (fig. 2 *e*). Setae are absent. A tail-like process, presumably the cast skin of the first instar, is present at the posterior part of the body.

When the larva is about three days old,the body is wrinkled laterally and dorsally while its posterior end is narrower than the anterior. Constrictions are very apparent in the anterior part of the body. The shape is globular. The mandibles are well sclerotised and appear to be moveable. Granulations or white spots are apparent on the gut with numerous fatty globules inside them. The colour is yellowish-green and no tracheal system is visible. The larva now measures 0·47 mm. in length and 0·24 mm.in width.

Third-stage larva (fig. 2 *f*).

About four days after hatching this stage has more white spots distributed mainly on the wall of the gut ; the gut itself is full of greenish-yellow granules and fat-like globules. The mandibles are stout, of a light-brown colour and are sickle-shaped. A slit-like opening representing the mouth is visible. The body is ovoid in shape and the body-wall, which has numerous translucent granules, shows folds or wrinkles. The larva measures 0·51 mm. in length and 0·32 mm. in width.

When the larva is about five days old the white spots have again increased considerably in number, and are more apparent and numerous in the posterior part of the body. The anterior part of the body has constrictions which suggest rudiments of division into head and thoracic segments. The mandibles (fig. 2 *g*) are smooth, swollen at the base and measure 0·19 mm. in length and 0·006 mm. in width.

About six days after hatching the white spots disappear and three conspicuous wrinkles develop at the anterior end and four at the posterior end. The last instar is now reached. The form of the prepupa is as shown in fig. 2 *h*, and the skin of the third moult is sometimes attached to it. No tracheal system is evident.

Pupa (fig. 2 *i*).

Translucent, smooth and pale-brown in colour, and the cuticle is thin and transparent. The abdominal segments are not clearly defined. The wing pads are distinct. The ocelli are slightly red and the leg joints well-defined. The length is 0·36–0·44 mm. and the width 0·18–0·23 mm.

Adult.

The adult of *T. australicum* was described by Girault (1912). Wings and antennae are shown in fig. 2 *j–m*. One of the characters given by Girault is the presence of the curved oblique line of discal cilia leading back from the stigmal vein (fig. 2 *j*). The number of cilia recorded by Girault is " not more than three, usually two but sometimes five ". As a result of the examination of a long series of specimens of the species now under consideration, it was found that this character is very variable. The number of cilia was found to vary from three to six and in one specimen one wing had four cilia and the other five. The fore-wing measures 0·47–0·57 mm. in length and 0·22–0·30 mm. in breadth ; it bears 9 to 15 longitudinal lines of discal cilia. The neuration extends for more than half the wing length and the longest cilia of the wing are about one-eighth its greatest width. The hind-wing measures 0·36–0·43 mm. in length and 0·04–0·05 mm. in breadth ; its longest cilia are about two and a half times it breadth.

The average length of the male is 0·56 mm. (maximum 0·70, minimum 0·46 mm.) and that of the female is 0·63 mm. (maximum 0·75, minimum 0·50 mm.). In general, the male is slightly smaller than the female from the same host.

Life-history.

Copulation generally occurs a few hours after emergence and lasts for 1–2 minutes on the average. A maximum of 10 minutes was observed. The female, when abundantly supplied with host eggs, starts oviposition in the first 24 hours after emergence and continues to do so for 2–3 days. The total number of eggs laid by a fertilised female is about 40, while a maximum of 65 has been observed. Dissections of fertilised females showed that, within 48 hours after emergence, at least 65 per cent. of the eggs are mature.

Superparasitism is common. Parasitised *Proceras* eggs collected in the field usually yielded three adults each, while from eggs of *Olethreutes schistaceana* two were usually obtained. The number of parasites capable of developing within a single host egg seems to be dependent upon its size, for in the laboratory as many as 17 parasite eggs have been laid in a single *Proceras* egg, and while nearly all hatched, the number of parasites that completed their development was always about three.

The duration of life of the adults, when confined in tubes without host eggs, varies with the temperature and humidity. At 24°C. and 80 per cent. relative humidity, it is about three days in the absence of food, and 5–8 days when raisins are provided. At 32°C. and 70 per cent. relative humidity adults live only two days without food and a maximum of four days when fed.

Oviposition occurs only in host eggs that are less than 3–4 days old. The larvae move actively after hatching and the contents of a host egg are completely consumed after 3–4 days in summer, irrespective of the degree of superparasitism. The durations of the various stages at different times of the year were determined in the laboratory in *Proceras* eggs and found to be as follows :—

TABLE IV.

Durations of the various stages of development of *Trichogramma* sp. ? *australicum*.

	Feb. to March (days)	April to May (days)	June to July (days)
Egg	1	2	2
1st larval stage	3	4	2
2nd larval stage			2
3rd larval stage			6
Prepupal stage	1	1	3
Pupal stage	4	4	7
Egg to adult	9	11	22
Mean temperature	23·4°C.	20·7°C.	17·9°C.

Parasitised eggs generally become black after five or six days owing to pigment which accumulates in the vitelline membrane. The number of exit holes in an egg is rarely more than two.

Parthenogenesis.

Parthenogenesis occurs and the progeny are male, but the fecundity of unfertilised females seems to be reduced, for with 12 virgin females the average number of eggs laid was eight, whereas with mated females under the same conditions it was 40.

Hosts.

D'Emmerez de Charmoy (1917) recorded *Proceras* and *Sesamia* as hosts of *Trichogramma australicum* in Mauritius. This is confirmed by the present work, although parasitism of *Sesamia* eggs is extremely rare, for of all those collected during the course of this work (see section on *Platytelenomus*) only one batch was parasitised.

Collections of other Lepidopterous eggs revealed the following additional hosts:—

TABLE V.

Species	Food-plant	No. of eggs collected (April to June)	No. of eggs parasitised	Percentage parasitism
Autographa chalcytes	Tomato	542	60	11·1
Achaea trapezoides	Castor Oil	540	297	55·0
Melanitis leda	Sugar-cane	368	66	18·0
Olethreutes schistaceana ...	Sugar-cane	150	13	8·9

It is to be noted that *Olethreutes schistaceana*, the white sugar-cane borer, is included, so that *Trichogramma* sp. ? *australicum* parasitises all three of the cane borers of Mauritius.

Natural Parasitism of Proceras sacchariphagus *Boj.*

The beneficial value of this species as a parasite of *Proceras* has already been discussed (Moutia & Mamet, 1945).

Maximum parasitism was found to occur during the winter season, April to September. The highest percentage parasitism found was 55·1 and the annual mean, based on three years' observations, was 5·9 per cent. The mean percentage of eggs parasitised per parasitised cluster was 87, with a mean number of 23·4 eggs per cluster.

The distribution of parasitised *Proceras* eggs in cane fields is very erratic. Within small areas of about 50–60 yards in diameter they are sometimes quite common, while in adjacent areas parasitism is nil even though host eggs are plentiful.

It is possible that the longer life-cycle of *Proceras* is a factor which tends to suppress the general incidence of parasitism, for this host has definite generations, although these are sometimes not clearly defined, and the fluctuations in the number of host eggs available may hinder the building up of the parasite population. The large-scale destruction of *Proceras* larva and pupae during the cropping season would have a similar effect by causing a subsequent sharp decline in the number of eggs available.

Trichogramma sp.

The collections of Lepidopterous eggs revealed a second species of *Trichogramma* parasitising the following hosts : *Sesamia* and *Olethreutes* on sugar-cane, *Autographa chalcytes* on tomato and *Achaea trapezoides* on *Acalypha* sp. This species (fig. 2 *n–q*) is closely related to *Trichogramma nana* (Zehnt.) and is easily distinguishable from *T. australicum* Gir. by the long marginal cilia of the fore-wings and by the more distinctly segmented antennae of the male.

During the summer months of November–December, 64·7 per cent. of *Olethreutes* eggs were found parasitised by this species and on the same host in winter, June–July, only 10 per cent. parasitism was recorded. This species was found in January parasitising 0·5 per cent. of *Sesamia* egg clusters, and *Autographa* and *Achaea* eggs were parasitised to the extent of 2 per cent. and 10 per cent., respectively, during the period of June–August.

This species would not parasitise *Proceras* eggs in the laboratory, which confirms that it is distinct from *T. nana*, for van der Goot (1915) records *Proceras* as a host of the latter in the Netherlands Indies.

LARVAL PARASITES.

Apanteles flavipes (Cameron) (Hym., Braconidae).

This species was described by Cameron (1891) from Poona (India) and has been redescribed by Wilkinson (1928). Its geographical distribution and recorded hosts may be summarised as follows :

INDIA : *Proceras* (*Diatraea*) *venosata* (Walk.), *Sesamia uniformis* Dudgn., *Diatraea* (*Argyria*) *sticticraspis* (Hmps.) and *Chilo simplex* (Butl.) (Isaac, 1940).

CEYLON : *Chilo zonellus* (Swinh.) (Vinson, 1942).

FORMOSA : *Eucosma schistaceana* (Sn.), *Diatraea venosata* (Walk.), *Chilo infuscatellus* Sn., *Sesamia inferens* (Walk.), *Cirphis loreyi* (Dup.), and *Chilo simplex* (Butl.) (Watanabe, 1932 ; Takano, 1934).

JAPAN : *Chilo simplex* (Butl.) (Watanabe, 1932).

QUEENSLAND : *Pragmatiphila truncata* (Walk.) (Bell, 1934).

MALAYA : *Diatraea auricilia* (Dudgn.) and *Diatraea* sp. (Pagden, 1930 ; Wilkinson, 1930) ; *Diatraea polychrysa* Meyr. (Corbett & Miller, 1933).

MAURITIUS : *Proceras sacchariphagus* Bojer (d'Emmerez de Charmoy, 1917).

Egg (fig. 3 *a*).

The egg, just after deposition, measures 0·136 to 0·140 mm. in length and 0·034 to 0·040 mm. in width. It is almost transparent, rounded at the cephalic end and enlarged medially, and it tapers posteriorly. There is a small button-like peduncle at the posterior end which measures about 0·0076 mm. in length. The chorion is smooth, thin, transparent and has no surface sculpture. During incubation, the egg gradually increases in size and becomes almost globular, measuring about 0·8 mm. in diameter. The embryo at this time is plainly seen in a somewhat curved position (fig. 3 *b*).

First-stage larva (fig. 3 *c*).

The newly hatched larva is vermiform and measures about 0·75 mm. in length and about 0·18 mm. at its greatest width. The head is as broad as long and bears unsclerotised hook-like mandibles (fig. 3 *d*), which measure 0·034 mm. in length and are 0·017 mm. wide at the base. The body consists of 12 ring-like segments, each of which except the last bears a transverse row of setae dorsally and laterally ; the setae are inclined backwards. The fully grown first-stage larva shows a caudal evagination which later develops into an anal vesicle. The larva at this stage is milky-white, translucent and measures from 0·79 mm. to 0·94 mm. in length and from 0·18 mm. to 0·27 mm. in width. The demarcation line between the head and the thorax is just discernible. Antennae and tracheae are not visible.

Second-stage larva (fig. 3 *e*).

The larva is cylindrical and the head and 13 segments are distinguishable ; the last segment is enlarged into a rounded anal vesicle which is slightly larger than the preceding segment. A caudal horn-like process is visible in some individuals together with a ring-like encircling band, immediately in front of the anal vesicle, which is the exuvia of the first moult. As in the first-instar larva, each body segment, except the anal one, bears a transverse row of setae dorsally and laterally. The cuticle bears scale-like processes as described for the last instar. The head is unsclerotised and bears simple and colourless mandibles ; these are smooth, broad basally and measure 0·046 mm. in length and 0·18 mm. at their base. Spiracles are absent and the tracheal system is as described for the third instar. The alimentary canal is not easily seen. The size of the larva varies from 1·05 to 1·23 mm. in length and 0·19 to 0·22 mm. in width ; the mean dimensions are 1·07 mm. long and 0·20 mm. wide.

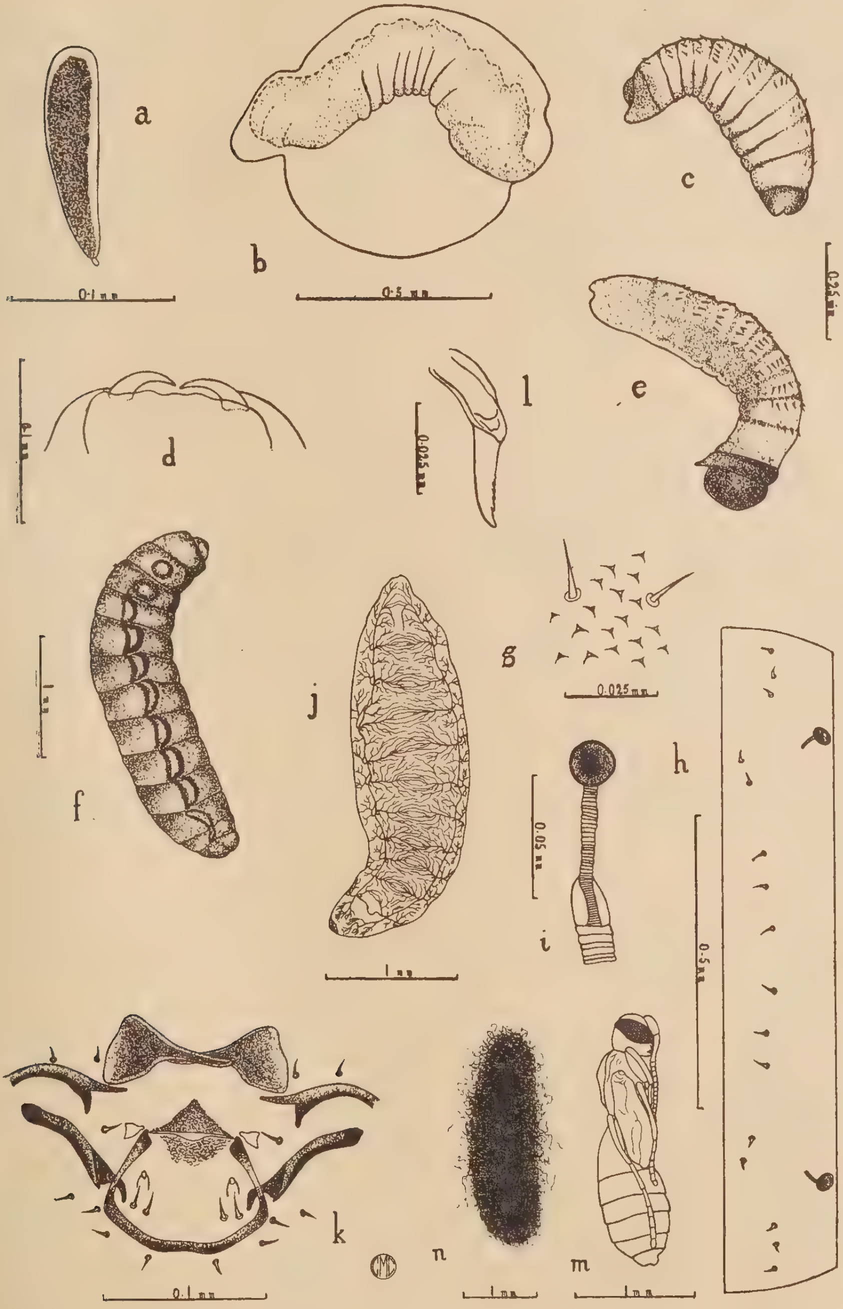
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Fig. 3.—*Apanteles flavipes* (Cam.) : *a*, egg ; *b*, egg prior to hatching showing embryo ; *c*, mature first-stage larva ; *d*, mandibles ; *e*, second-stage larva with caudal vesicle ; *f*, third-stage larva ; *g*, cuticular structure ; *h*, setal map of third post-cephalic segment ; *i*, spiracle ; *j*, tracheal system ; *k*, cephalic skeleton ; *l*, mandible ; *m*, pupa ; *n*, cocoon.

Third-stage larva (fig. 3 *f*).

After emerging from its host, the third-stage larva is creamy-white and grub-like, and measures from 2·57 to 3·15 mm. in length and 0·67 to 0·78 mm. in width, the average dimensions being 2·92 mm. in length and 0·72 mm. in width. The segmentation is distinct, and the body tapers slightly anteriorly and posteriorly ; the anal vesicle is completely retracted. A small lateral hump is visible on the mesothorax and metathorax. Abdominal segments 1 to 9 bear hypopleural swellings ; there is no hump on the dorsal surface. The cuticle is shiny and translucent. Part of the cuticle of the head and body is minutely studded in a scale-like manner (fig. 3 *g*), and each of the first 12 segments bears a row of stout spines ; the last segment is without spines. The setal map of the third post-cephalic segment is shown in fig. 3 *h*. The larva has 8 pairs of open spiracles, one pair near the anterior margin of the mesothorax and one pair near that of each of the first 7 abdominal segments. A spiracle is shown in fig. 3, *i*, and the tracheal system in fig. 3 *j*.

The tracheal trunks are joined anteriorly in the prothorax by a transverse dorsal commissure and are unconnected posteriorly. The two main lateral trunks further give rise dorsally and ventrally to secondary branches which ramify extensively in each segment. The head and penultimate abdominal segment are supplied with secondary branches leaving the extremities of the main trunks.

The cephalic skeleton (fig. 3 *k*) is well developed and bears a sclerotised buccal armature. The dorsal region of the head bears very minute spines. The mandibles are light-brown and are shaped as in fig. 3 *l* ; they bear four minute teeth and measure 0·087 mm. in length and 0·053 mm. in width. The epistoma is not distinct and numerous paired sensory setae are distributed on the labral and labial areas. The maxillary region bears a rudimentary sensory papilla and has a single large seta. The labium is enclosed in a well defined ring and bears two rudimentary palpi or tubercles and two pairs of setae. No antennae could be found.

Pupa (fig. 3 *m*).

White at first and gradually darkens to light-brown. It measures 2·2 mm. in length and 0·76 mm. in width. It is enclosed in a snowy-white cocoon which is cylindrical in shape and measures 3 to 3·5 mm. in length and 1 to 1·5 mm. in diameter (fig. 3 *n*).

Adult.

The reader is referred to Wilkinson's redescription of the species (1928), and to the supplementary description of the head by Bhatnagar (1950).

Life-history.

The adults are very active soon after emergence from the cocoons and readily start feeding, pairing and ovipositing. In cane fields, they are generally found in bright sunlight seeking *Proceras* larvae which are either in tunnels in cane stems or exposed outside their galleries in dried leaf sheaths prior to pupation.

Copulation lasts from 1–2 minutes and oviposition from 25–45 seconds.

The female, after inserting the ovipositor into a host, lays 60–65 eggs in succession. The eggs may be deposited in any part of the body cavity of the host larva. Parasitised larvae continue their normal activities until the parasite larvae are about to leave them, when they become moribund ; they remain alive for 2–4 days after all the parasites have emerged from them. In the field, parasitised *Proceras* larvae were of the later instars. In some rare cases, larvae found parasitised were in the prepupal stage.

The average number of mature eggs found in fertilised females on dissection was 137 ; this figure represents two thrusts of the ovipositor at 60–65 eggs per thrust. Oviposition is generally restricted to two days after emergence and mating, and the total number of eggs laid during the life of the female in summer was found to average 262. The length of life of the adults is shown in Table VI. All were kept in tubes measuring 6×1 ins. and allowed to oviposit ; those fed were given raisins.

TABLE VI.

	Length of life in summer (December to March)		Length of life in winter (June to August)	
	Fed	Unfed	Fed	Unfed
Male	3–5 days	2½ days	7–10 days	1½–2 days
Female	2–3 days	1 day	3– 4 days	2 –2½ days
	Temperature 28–30°C. R. humidity 60–70 per cent.		Temperature 18–20°C. R. humidity 76·5–82·5 per cent.	

Dissections of field-collected *Proceras* larvae showed that the number of *Apanteles* larvae per host varied from 23 to 125, the average being 44. As the number of eggs laid at one thrust of the ovipositor averaged 63 in tests made with 50 females, it would appear that only about 75 per cent. of the eggs laid reach the final larval stage. When the larvae leave their host, they are in the last instar, and they spin their cocoons within 24 hours. The prepupal stage follows within 48 hours after completion of the cocoon and is of short duration.

The cocoons are spun on and around the host larva and are generally found as a white mass. The number of adults obtained per parasitised larva was, on the average, 42·6, the maximum being 98. The proportion of males to females from field-collected cocoons was 1 : 2·5 in a total of 2,467 individuals. The highest proportion of females obtained from a single mass of cocoons was 5·6 to one male.

Parthenogenesis.

Parthenogenetic reproduction sometimes occurs in the field, as five of 66 batches of cocoons collected yielded only male progeny. Laboratory breedings with virgin females confirmed this field observation.

Table VII shows the life-cycle of this parasite when bred on *Proceras* in the laboratory.

TABLE VII.

Life-cycle of *Apanteles flavipes* on *Proceras sacchariphagus.*

	Summer (January to March)		Winter (July to August)	
	Duration (days)	Mean duration (days)	Duration (days)	Mean duration (days)
Incubation	2–3	2·5	4–5	4·5
1st-stage larva ...	3–4	3·5	10–15	12·5
2nd-stage larva ...	4–5	4·5		
3rd-stage larva ...	2–3	2·5		
Prepupa	1–2	1·5	10–14	12
Pupa	4–6	5·0		
Total	16–23	19·5	24–34	29
Mean temperature ...	23·4°C.		17·5°C.	

Hosts.

During a survey which was carried out over more than two years, no host other than *Proceras sacchariphagus* was found although over 8,500 larvae of *Sesamia* and 2,000 of *Olethreuetes* were dissected. Attempts to breed the parasite on *Sesamia* failed ; in two instances, oviposition did occur but the parasite larvae died before reaching the second instar. It is interesting to note that *Apanteles flavipes* behaves differently in Formosa and India, where amongst its recorded hosts are the Noctuids, *Sesamia inferens* (Walk.), *S. uniformis* Dudgn. and *Cirphis loreyi* (Dup.) (Watanabe, 1932 ; Takano, 1934 ; Isaac, 1940).

Natural parasitism of Proceras sacchariphagus.

The incidence of this parasite on *Proceras* was worked out by collecting and dissecting host larvae from various regions of the island where *Proceras* infestation was high. Table VIII shows the percentage parasitism over a period extending from April, 1949, to March, 1951.

TABLE VIII.

Percentage parasitism of *Proceras sacchariphagus* by *Apanteles flavipes*.

Months	No. of larvae dissected	No. of larvae parasitised	Percentage parasitism
April–May 1949	410	68	16·5
June–July ,, ...	821	166	20·2
August–September 1949	695	44	6·3
October–November ,, ...	641	34	5·3
December 1949–January 1950 ...	437	10	2·3
February–March 1950	982	26	2·6
April–May ,, ...	936	5	0·5
June–July ,, ...	297	16	5·4
August–September 1950	1,014	116	11·4
October–November ,, ...	333	26	7·8
December 1950–January 1951	292	10	3·4
February–March 1951	130	7	5·4
Total	6,988	528	—

Mean percentage parasitism (from totals above) : 7·5.

Jepson (1939) has recorded 50–60 per cent. parasitism, but does not state the number of host larvae he collected. Such a high figure was obtained occasionally with small collections of larvae but the above Table suggests that it does not represent the general incidence of parasitism.

Owing to the erratic seasonal distribution of this parasite in the field and its rather low yearly incidence, it can hardly be considered of great economic value. Amongst the factors which may limit its beneficial effect are the short duration of life of the adult in summer, when the host is rare, and hyperparasitism, which to some extents limits its abundance in cane fields.

Hyperparasite of *Apanteles flavipes*.

Calliceras sp. (? *fijiensis* Ferrière).

This Ceraphronid was recorded during the present work as a hyperparasite of *Apanteles flavipes* (Cam.) and of a species of *Apanteles* attacking larvae of *Nacoleia praeteritalis* Walk. Williams (1951b) recorded it in Mauritius as a secondary parasite of *Brenthia leptocosma* Meyr. probably through the primary parasite *Microgaster curticornis* Granger. *Calliceras fijiensis* Ferrière has been recorded in Fiji and the Solomon Islands from *Apanteles tirathabae* Wlkn. (Ferrière, 1933).

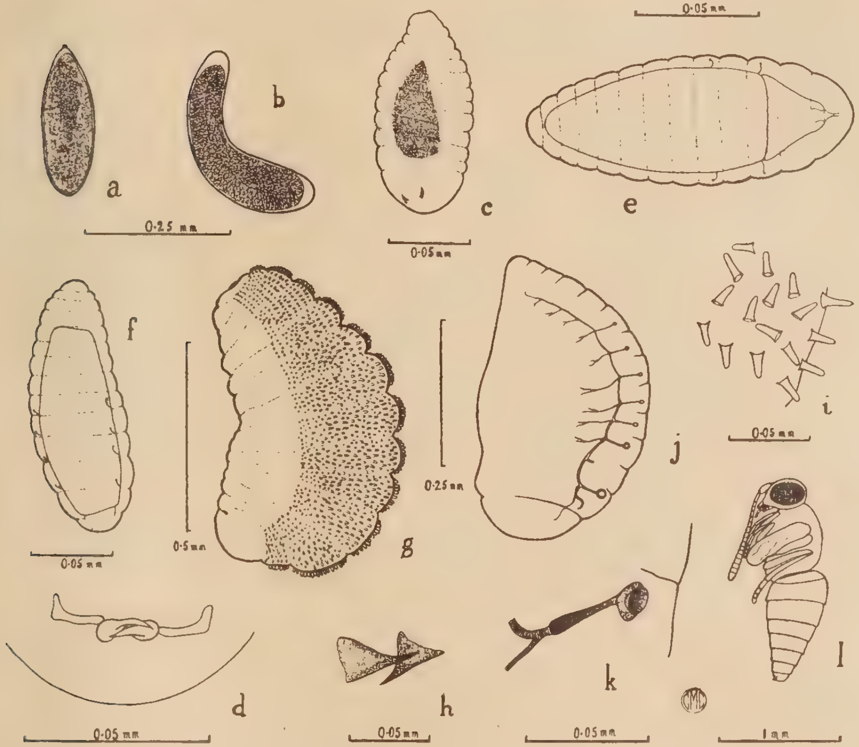

Fig. 4.—*Calliceras* sp. ? *fijiensis* Ferrière : *a*, egg, newly laid ; *b*, egg, before hatching ; *c*, first-stage larvae ; *d*, mandibles ; *e*, tracheal system ; *f*, second-stage larva ; *g*, third-stage larva ; *h*, mandibles ; *i*, cuticular structure ; *j*, tracheal system ; *k*, spiracle ; *l*, pupa.

Egg (fig. 4 *a*).

White, transparent and elongate oval, broader at the anterior end and bears a minute nipple-like protuberance at the posterior end. The chorion is smooth and shiny. When freshly laid, the egg measures 0·26 mm. in length and 0·09 mm. in width. During incubation it increases considerably in size and eventually measures 0·34 mm. in length and 0·09 mm. in width ; it is then sausage-shaped (fig. 4 *b*).

First-stage larvae (fig. 4 *c*).

White and translucent. The head is broadly rounded and the body is clearly 12-segmented, the largest segment being the first abdominal. The position of the mandibles with the mandibular struts is as shown in fig. 4 *d* ; the mandibles are finely pointed and unsclerotised, and they measure 0·019 mm. in length and 0·0045 mm. at the base. The integument is shiny and has very minute papillae on the dorsum ; these are arranged in transverse rows and are visible only under high magnification. The respiratory system consists of tracheal trunks united by transverse commissures anteriorly and posteriorly. Two pairs of open spiracles are present, one on the mesothorax and the other on the first abdominal segment (fig. 4 *e*).

Second-stage larva (fig. 4 *f*).

Resembles the first stage, but has one more segment and four pairs of spiracles which are situated near the anterior margins of the second and third thoracic and first and second abdominal segments. The larva measures 0·44 mm. in length and 0·27 mm. in width at its broadest part. The mandibles measure 0·03 mm. in length and 0·0076 mm. in width at their base.

Third-stage larva (fig. 4 *g*).

Creamy-white in colour and opaque. The body is elongate-oval or pear-shaped, robust, broadest at the third thoracic segment and slightly curved. The head is relatively small, smooth and situated ventrally. The mandibles (fig. 4 *h*) are simple, pointed and lightly sclerotised, and they measure 0·06 mm. in length and 0·034 mm. in width at the base. Tubercles or conical papillae (fig. 4 *i*) are present on the dorsum and sides of all body segments except the last, which is smooth and rounded. There are seven pairs of spiracles (fig. 4 *j*), one pair near the posterior margin of each segment from the first thoracic to the fifth abdominal, except the second thoracic. Those on the first thoracic segment are the largest. There is a tracheal branch with no spiracle between the first and third thoracic segments. The spiracles (fig. 4 *k*) have a stout peritreme measuring 0·01 mm. in diameter. The fully developed larva measures 1·40 mm. in length and 0·65 mm. in width at its broadest part. The cephalic skeleton is not very apparent and only the mandibles and their faint struts are visible under high magnification.

Pupa (fig. 4 *l*).

Dirty-white in colour, smooth and shiny ; the segmentation is not very apparent on the thorax but is well marked in the abdominal region. The eyes and ocelli are light-brown in colour. Length 1·5 mm. and width at thorax 0·54 mm.

Adult.

For the description of *Calliceras fijiensis* reference should be made to Ferrière (1933).

Life-history.

Adults, on emergence from cocoons of *Apanteles flavipes*, copulate within a few seconds. When supplied with plenty of host cocoons and raisins as food, the female starts ovipositing shortly after copulation. The eggs are laid in the cocoon but outside the pupa, and are not attached. On hatching, the larva crawls on the body of the pupa and adheres to the dorsum of the last thoracic segment or the anterior abdominal segments. It develops ectoparasitically. Feeding is completed at the end of the third instar, causing the collapse of the integument of the host. A meconium is passed in the prepupal stage.

When supplied with food and plenty of host cocoons, in breeding tubes measuring 6×1 ins., *Calliceras* females generally laid most of their eggs during the first 12 days after emergence. The total number of eggs laid per female averaged 36 and the number of eggs laid per day varied from one to eight, the mean being 2·5. The minimum number of mature eggs found in females on dissection was 12 and the maximum 26.

The average number of *Calliceras* adults obtained per *Apanteles* cocoon was four, and the maximum from one cocoon was 12.

The duration of adult life in summer (December–March, mean temperature 24°C.), when the insects were fed on raisins, kept in tubes and allowed to oviposit, averaged 28 days, the maximum being 41 days. Without food, under otherwise similar conditions, the adult life was 4–6 days only. The sex ratio was 1 male to 3·2 females in 204 individuals. Parthenogenesis was not observed.

The life-cycle is shown in Table IX.

The long period between December and July, when no parasitised *Apanteles* cocoons were obtained, indicates that this hyperparasite must have other hosts in the field ; one alternative host, a species of *Apanteles* parasitising *Nacoleia praeteritalis*, has been recorded above.

TABLE IX.

Life-cycle of *Calliceras* sp. ? *fijiensis* on *Apanteles flavipes.*

	November—February (days)	July—August (days)
Incubation	2	3
1st larval stage	8·5	10
2nd larval stage		
3rd larval stage		
Pupal stage	4·5	20
Total	15	33
Mean temperature	23·5°C.	18·0°C.

Table X shows the rate of parasitism in field-collected *Apanteles* cocoons.

TABLE X.

Percentage batches of *Apanteles* cocoons parasitised by *Calliceras* ? *fijiensis.*

	No. of batches of cocoons collected	No. of batches of cocoons parasitised	Percentage parasitism
January	8	0	Nil
February	5	0	Nil
March	Nil	Nil	Nil
April	Nil	Nil	Nil
May	6	0	Nil
June	4	0	Nil
July	20	1	5
August	82	4	4·9
September	48	1	2·1
October	22	1	4·5
November	11	1	8·9
December	10	1	10
Total	216	9	—

Mean percentage parasitism (from totals above) : 4·1.

Enicospilus sp.

The Ichneumonids previously recorded as larval parasites of *Sesamia vuteria* and *Proceras sacchariphagus* in Mauritius are *Enicospilus antancarus* (Sauss.) and *E. mauritii* (Sauss.) (Bordage, 1898 ; d'Emmerez de Charmoy, 1917 ; Moutia, 1934).

We have not obtained either of these species. *E. mauritii*, which was validated and has often been referred to as *Ophion mauritii*, has recently been bred from larvae of *Cirphis loreyi* (Dup.), in cane fields (Williams, in press), but in laboratory tests it did not parasitise larvae of *Sesamia* or *Proceras.*

During the present survey, 150 specimens of *Enicospilus* were reared from field-collected *Sesamia* larvae. These belong to a different species. At the present time, this cannot be specifically named and must therefore be designated as *Enicospilus* sp. ; the wings are shown in fig. 5 *p*, and attention is particularly drawn to the pattern of the scleromes in the discal cell.

No Ichneumonid was obtained from *Proceras* larvae, despite the earlier records. To check these findings, *Proceras* larvae were confined with specimens of the species of *Enicospilus* obtained from *Sesamia*, but no parasitism occurred.

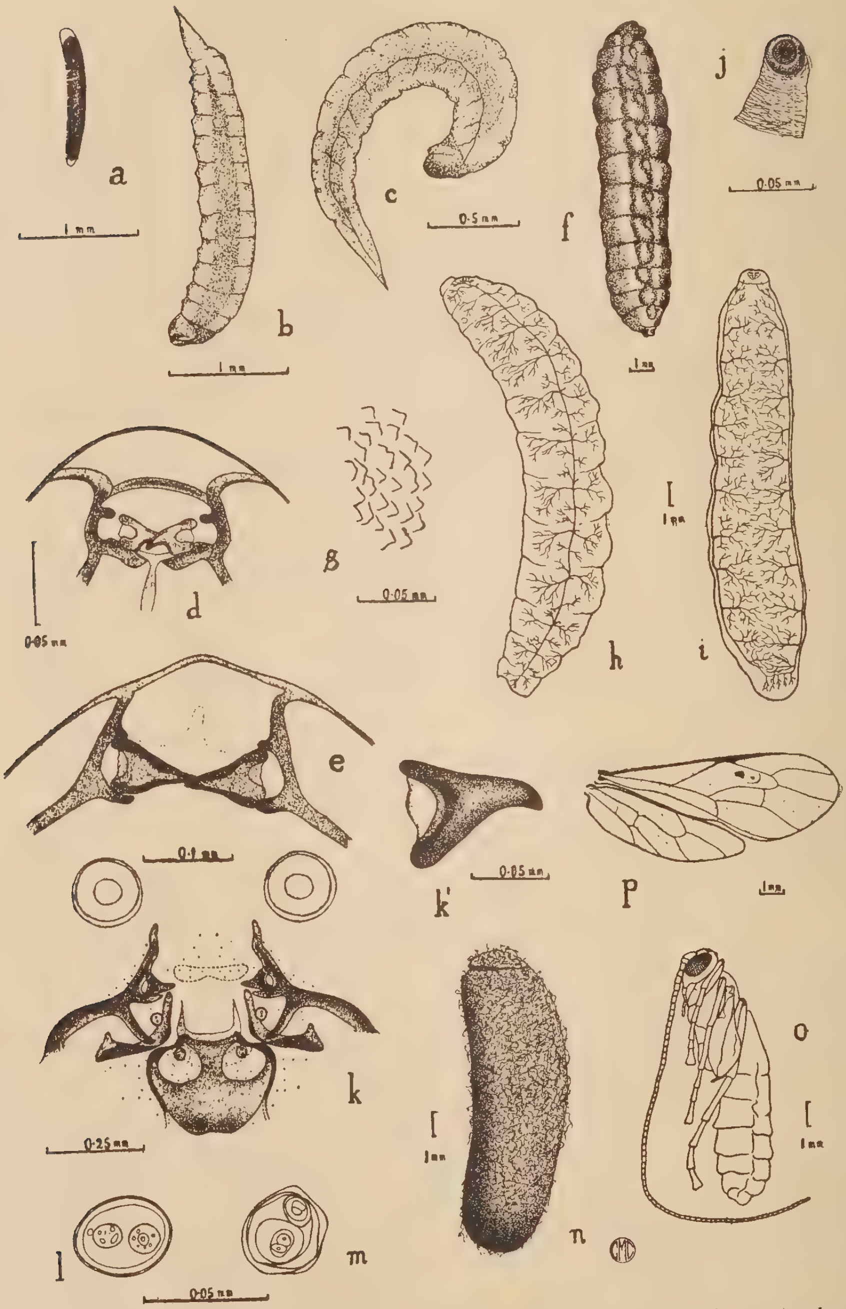
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Fig. 5.—*Enicospilus* sp. : *a*, egg ; *b*, first-stage larva fully developed ; *c*, tracheal system ; *d*, cephalic skeleton and mandibles ; *e*, second-stage larva, cephalic skeleton and mandibles ; *f*, third-stage larva, fully developed ; *g*, cuticular structure ; *h*, tracheal system, lateral view ; *i*, tracheal system, ventral view ; *j*, spiracle ; *k*, head skeleton ; *k'*, mandible ; *l*, maxillary sensilla ; *m*, labial sensilla ; *n*, cocoon ; *o*, pupa ; *p*, wing pattern.

Egg (fig. 5 *a*).

Dirty-white to light-brown in colour, cylindrical in shape and slightly curved ; its ends are uniformly rounded. The chorion is smooth and unsculptured. The egg measures 1·07 mm. in length and 0·16 mm. in width.

First-stage larva (fig. 5 *b*).

Creamy-white and translucent. The body is cylindrical and the last segment ends in a tail-like process the length of which is less than one-third of that of the body. The head is not sclerotised and there are 13 distinct body segments. The mandibles are simple and pointed, without teeth, and measure 0·05 mm. in length and 0·03 mm. in width at the base. The cuticle is smooth and bears no setae. On each of the body segments 2 to 12, there is a pair of ventro-lateral projections, these being more developed in segments two to four than in the others. The tracheal system (fig. 5 *c*) consists of a longitudinal trunk on each side of the body, and the trunks are united posteriorly by a ventral commissure ; they are not connected anteriorly. The lateral accessory trunks which are common in Ichneumonid larvae are absent. There are no spiracles. The head skeleton and mandibles are shown in fig. 5 *d*. Head measurements : length 0·25 mm., width 0·27 mm. The body, including the tail, is 2·7 mm. in length, and the tail 0·48 mm.

Second-stage larva.

Similar to the preceding stage except that the tail is considerably shorter, the body segments are more clearly defined and the mouth opening is more ventrally placed. The cuticle is shiny and minutely papillose as in the third stage. The ventro-lateral projections present in the first stage have disappeared. The tracheal system is more distinct, but lateral accessory trunks are not apparent in segments two and three. Spiracles are absent. The mandibles are slightly sclerotised and measure 0·09 mm. in length and 0·06 mm. at the base. Length of head, 0·5 mm. ; width, 0·8 mm. Length of body and tail, 6·5 mm. ; length of tail 0·32 mm. The head skeleton is as shown in fig. 5 *e*.

Third-stage larva (fig. 5 *f*).

Dirty-white in colour with brown facial rods, and nearly opaque except at the anterior and posterior extremities. It is cylindrical in shape and tapers slightly towards the posterior end ; when viewed dorsally, it appears to be elliptical in outline. A dorsal hump is visible on segments 7 to 11, and segments 3 to 11 bear prominent transverse lateral folds or humps. Segments 1 to 3 bear small paired papillae ventrally. The body is broadest at abdominal segments three, four and five. When fully extended, the larva measures 13–15 mm. in length, 3·5–4 mm. in width and 3–3·5 mm. in thickness. The anal segment is sunken dorsally and protrudes ventrally to form a small tubercle. The cuticle is smooth and shiny ; no setae or spines could be detected, but it is minutely papillose as shown in fig. 5 *g*. The tracheal system is shown in fig. 5 *h*, *i*. There is no tracheal commissure in the thoracic region. There are nine pairs of spiracles, one pair near the posterior margin of the first thoracic segment and one on each of the first eight abdominal segments. The spiracles are as shown in fig. 5 *j*. The atrium is almost spherical with a fine thickened ring and measures 0·038 mm. in diameter. The head skeleton is as shown in fig. 5 *k* ; the labial ring is sclerotised, but the labrum is not, and the lateral sclerotised structure bears condyles for the articulation of the mandibles. The latter are slightly pointed, sclerotised and without teeth, and measure 0·12 mm. in length and 0·099 mm. in width at the base. The maxillary and labial sensillae are shown in fig. 5 *l*, *m*.

Cocoon.

Oblong-oval in shape (fig. 5 *n*) and brown and felt-like. It measures 12 mm. in length and 2 mm. in width.

Pupa (fig. 5 *o*).

Creamy-white in colour ; the eyes are brown at the time of moulting.

Life-history.

Mating was observed in the field, in summer, between 8 and 9 a.m. and from 3 to 7 p.m. In the laboratory adults 3–5 days old mated in glass jars 12 ins. high and 5 ins. in diameter, in the sun. Copulation usually lasts about 2½ hours, but sometimes as long as 8 hours.

The pre-oviposition period was 8–10 days in December and January. Extreme difficulty was experienced in inducing the females to oviposit in the laboratory, and oviposition occurred on only a few occasions and then only when host larvae were presented in bagasse or finely cut cane stems. Oviposition cages of the type used by Bradley & Burgess (1934) for the study of *Cremastus flavoorbitalis* (Cam.) were tried but did not give better results. Dissections of field-collected host larvae showed that oviposition was most frequent in larvae in the fourth and fifth stages. Only one egg was found in the body cavity of the host larva. No signs of paralysis were observed in parasitised larvae. The mature larva of the parasite, on emerging from its host, is sluggish. The spinning of the cocoon is completed in 24–36 hours. In the field, cocoons are found in cane trash or on other vegetable débris.

Adults fed on raisins and honey-water remain alive for 20–35 days in glass jars 12 ins. high and 5 ins. in diameter, at 25–27°C. The sex ratio in 105 adults which emerged from field-collected host larvae was 2·3 males to 1 female. The total number of eggs laid per female could not be determined owing to the very erratic and poor oviposition of this parasite in the laboratory. In 36 females captured in the field and dissected, the mean number of mature eggs per female was eight, and the maximum ten ; the number of ovarioles was 14.

The duration of the various stages as obtained from the few successful laboratory tests is given in Table XI.

TABLE XI.

Life-cycle of *Enicospilus* sp. on *Sesamia vuteria.*

	December-January (days)	June-July (days)
Incubation period	2	3
1st larval stage	4	7
2nd larval stage	13	18
3rd larval stage		
Prepupa	8	10
Pupa	20	32
Total	47	70
Mean temperature	23·7°C.	18·0°C.

Natural parasitism.

Dissections of *Sesamia* larvae obtained from very highly infested localities were carried out systematically during one year with the results shown in Table XII.

The maximum parasitism never reached more than 9 per cent. when a large sample consisting of 200—300 larvae was taken. In only one instance, with a sample of 105 larvae, did the percentage parasitism reach 20. Parasitism is at its peak during the summer months. Adults are plentiful in cane fields at the same time of

TABLE XII.

Monthly percentage parasitism by *Enicospilus* sp. on *Sesamia* larvae.

Months	No. of larvae dissected	No. of larvae parasitised	Percentage parasitism
January	929	3	0·3
February	2,808	227	8·1
March	241	5	2·0
April	611	8	1·3
May	412	6	1·4
June	221	0	0
July	162	2	1·2
August	180	4	2·2
September	190	4	2·1
October	389	4	1·0
November	1,677	15	0·9
December	524	4	0·7
Total	8,344	282	—

Mean percentage parasitism (from totals above) : 3·4.

year ; at other times they are somewhat rare. The data in Table XII indicate that this parasite is not of great economic importance.

Nematodes.

A nematode of the genus *Mermis* was found to parasitise larvae of *Sesamia* and *Proceras* only during the wet months of March and April, when the percentage of *Sesamia* larvae parasitised was 20 and that of *Proceras* 15·5.

PUPAL PARASITES.

Tetrastichus sp.. (near *atriclavus* Waterst.) (Hym., Eulophidae).

This insect was submitted to the Commonwealth Institute of Entomology and identified as a member of the genus *Tetrastichus*, many species of which are no doubt still undescribed.

Egg (fig. 6 *a*, *b*).

Creamy-white in colour. It is smooth, shiny, translucent and tapering. The chorion is unsculptured. When freshly laid, the egg measures 0·25 mm. in length and 0·09 mm. in width. Before eclosion, it measures 0·33 mm. in length and 0·10 mm. in width.

First-stage larva (fig. 6 *c*).

Creamy-white in colour and fusiform ; it is broader anteriorly and tapers towards the posterior extremity. The head is hemispherical and there are 13 clearly defined body segments. The body is widest between the second and third thoracic segments. The integument is shiny and unsculptured. Each body segment, except the first, bears two rows of minute setae on its dorsal half. The mandibles (fig. 6, *l*) are unsclerotised and simple, and they measure 0·015 mm. in length and 0·007 mm. at the base. The tracheal system consists of two main longitudinal trunks extending from the second to the tenth segments. In the first segment, the two longitudinal trunks are connected by a transverse commissure dorsal to the gut and give off a pair of bifurcating branches to the head. Posteriorly, in segment 11, the longitudinal trunks are transversely connected by a commissure ventral to the alimentary canal. Nine pairs of rudimentary stigmatic tracheal trunks are present in the last two thoracic and the first seven abdominal segments. Spiracles are absent. The length of the larva at this stage is 0·38 mm. and its width is 0·11 mm. The head skeleton is as shown in fig. 6 *d*.

Second-stage larva (fig. 6 *e*).

Creamy-white and translucent. A dorso-lateral lobe is apparent on each segment from the first to the eleventh. The cuticle of the body is shiny and glabrous, and bears no external structures. The head is unsclerotised and smooth. The mandibles (fig. 6, *m*) are acutely pointed and unsclerotised, measuring 0·02 mm. in length and 0·025 mm. in width. Spiracles are absent. The tracheal system is similar to that of the previous instar with a slight increase in the size and length of the tracheal trunks and of the stigmatic trunks. The larva at this stage measures 1·25 mm. in length and 0·26 mm. in width.

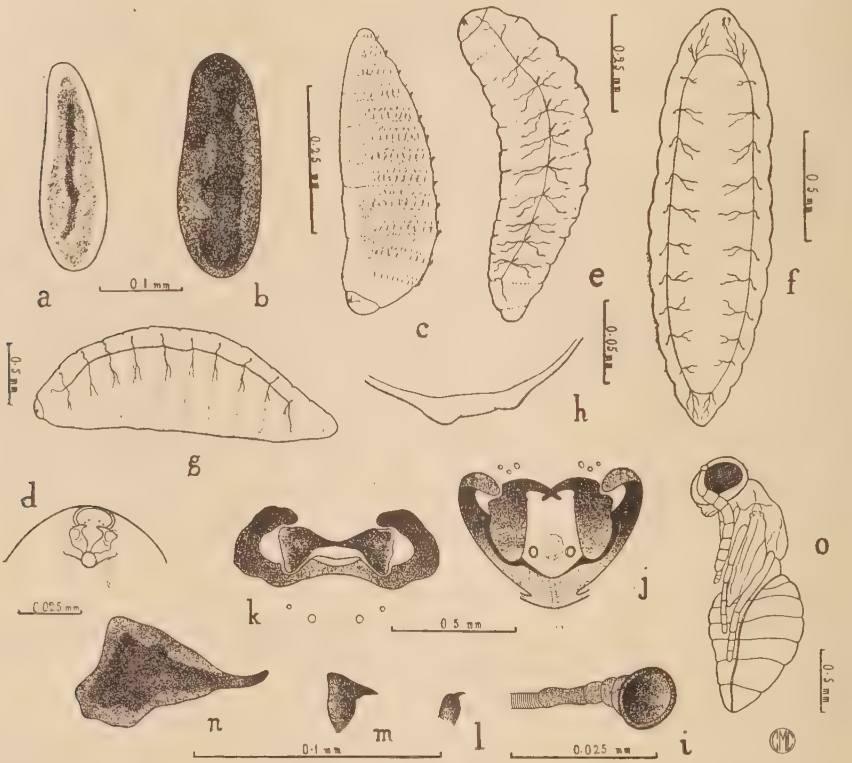


Fig. 6.—*Tetrastichus* sp. (near *atriclavus* Waterst.) : *a*, egg, freshly laid ; *b*, egg before hatching ; *c*, first-stage larva ; *d*, head skeleton ; *e*, second-stage larva with tracheal system ; *f*, third-stage larva with tracheal system, dorsal view ; *g*, the same, lateral view ; *h*, antennal processes ; *i*, spiracle ; *j*, head skeleton, front view ; *k*, the same, top view ; *l*, mandible, first-stage larva ; *m*, mandible, second-stage larva ; *n*, mandible, third-stage larva ; *o*, pupa.

Third-stage larva (fig. 6 *f*, *g*).

Dirty-white, opaque and fusiform. The head is narrow and the segmentation is distinct. The dorso-lateral lobes are not as conspicuous as in the second stage. The cuticle is shiny, glabrous and unsculptured. The antennal processes on the dorsal surface of the head are conspicuous and papilla-like. The tracheal system is similar to that of the second stage, except that the spiracles (fig. 6 *i*) are now developed and are connected to the former rudimentary trunks by short spiracular trunks. Nine pairs of spiracles are present, one pair on each segment from the second to the tenth. The peritreme is stout with an aperture of 0·012 mm. in diameter. A pair of short rudimentary tracheal trunks is present in segment 11. The average length of the fully extended larva is 2·5 mm. and the maximum width is 0·75 mm. The head capsule is as shown in fig. 6 *j*, *k*. The mandibles (fig. 6 *n*) are strongly arched and measure 0·076 mm. in length and 0·045 mm. in width at the base.

Prepupa.

White, transparent and shiny.

Pupa (fig. 6 *o*).

Light brown in colour and the segmentation is clearly apparent. The cuticle is transparent and shiny. The eyes and ocelli are brown. The length is 2·1 mm. and the width at the thorax is 0·64 mm.

Adult.

The adult agrees fairly closely with *Tetrastichus atriclavus* as described by Waterston (1915).

Life-history.

The males generally emerge 20–40 minutes before the females. The number of exit holes per parasitised pupa was on the average two, the maximum found being six. Copulation starts as soon as the females emerge and lasts for 30 to 60 seconds. Oviposition begins immediately afterwards if the female is provided with abundant host pupae and plenty of food. The eggs are deposited at random in the body cavity of the pupa. Young larvae can feed in freshly formed pupae undergoing histolysis or in more developed ones. When the larvae are at the end of their third instar, the contents of the pupa have generally been entirely consumed.

The total number of eggs laid per female averages 75, the maximum observed being 96. The egg-laying period extends from 10 to 20 days from the date of emergence of the female and the number of mature eggs found in dissected females varied from 17 to 51. With plenty of food and host pupae, a female lays about six eggs a day during the first 12 days ; subsequently, only one or two are laid each day.

The sex ratio was 1 male to 21 females in 503 individuals from field-collected material. The number of individuals that develop in a single pupa varies according to the size of the latter. Pupae of various Lepidoptera superparasitised by several females yielded the numbers of adult *Tetrastichus* shown in Table XIII.

TABLE XIII.

Species	Size of pupae	No. of *Tetrastichus* adults obtained
Nacoleia praeteritalis	9·5 mm. × 2 mm.	64
Olethreutes schistaceana	12·7 mm. × 2·5 mm.	110
Olethreutes rhynchias	12·6 mm. × 3·7 mm.	142
Proceras sacchariphagus	19·0 mm. × 3·9 mm.	186
Sesamia vuteria	20·2 mm. × 4·5 mm.	528

From field-collected pupae of *Proceras* and *Sesamia*, the usual number of adults obtained per pupa was between 20 and 60. In one instance, 541 adults were obtained from a *Sesamia* pupa.

The life-cycle of this parasite in the laboratory during the winter and summer months is given in Table XIV.

TABLE XIV.

Life-cycle of *Tetrastichus* sp. near *atriclavus* in *Sesamia.*

	December—March (days)	July—September (days)
Incubation period	1½	2
1st larval stage	1½	11½
2nd larval stage	3	
3rd larval stage	4½	
Prepupal stage	1	13½
Pupal stage	4½	
Total	16	27
Mean temperature	23·9°C.	18·2°C.

The duration of life of adults in summer was determined in tubes (6 × 1 ins.) with and without food and with plenty of host material for oviposition. Table XV summarises the results.

TABLE XV.

Duration of life of adults in summer (December-March, mean temperature 23·9°C.).

	With food		Without food	
	Minimum (days)	Maximum (days)	Minimum (days)	Maximum (days)
Male	12	24	3	5
Female	13	38	5	13

Parthenogenesis.

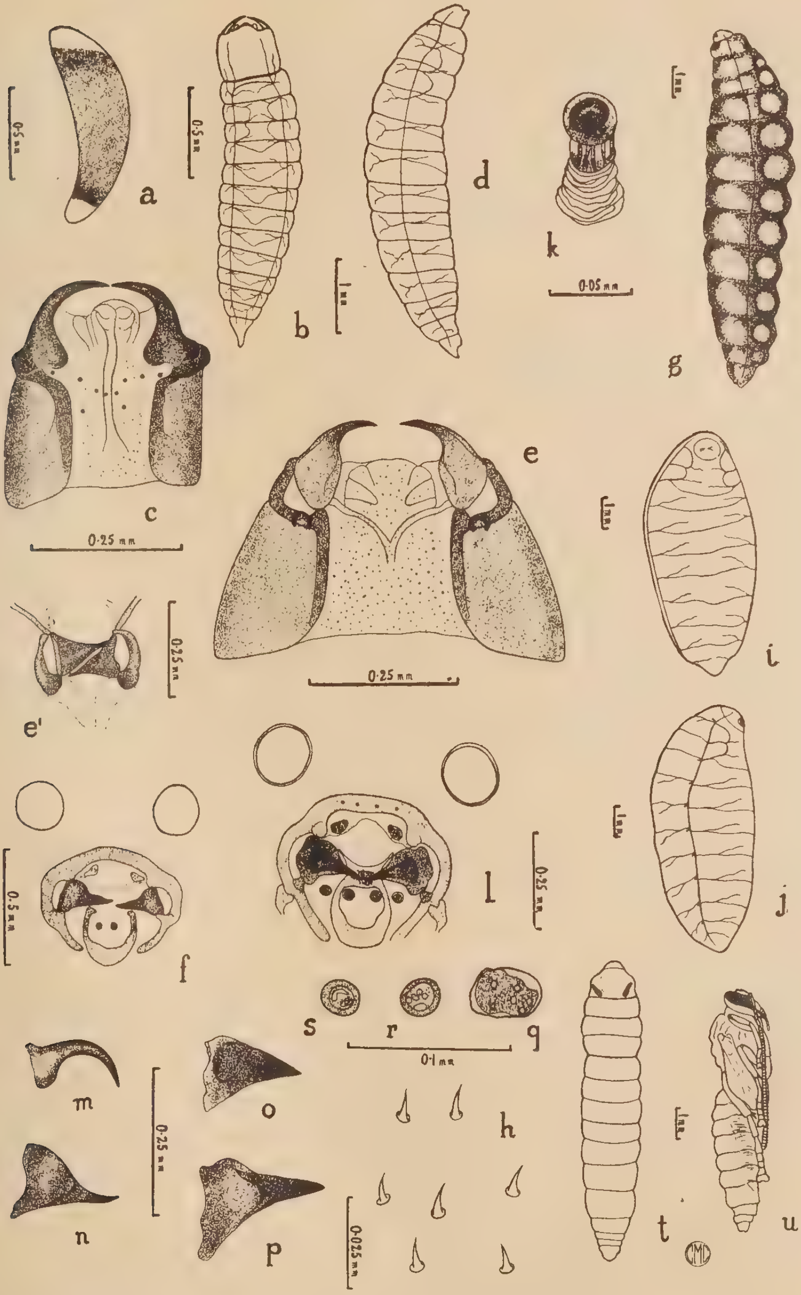
This was investigated in the laboratory with ten virgin females which were amply provided with host pupae. The progeny obtained were invariably male and the mean number of males obtained from a parasitised pupa was 89.

Hyperparasitism was once recorded with a field collected pupa of *Sesamia vuteria.* The host pupa had been previously parasitised by *Xanthopimpla stemmator* (Thunb.) which had developed up to the pupal stage before being attacked by *Tetrastichus.*

Natural Parasitism.

The natural incidence of this insect as a parasite of *Sesamia* and *Proceras* pupae is not easy to assess owing to the difficulty of collecting adequate numbers of host pupae. Of a total of 822 pupae of *Proceras* and *Sesamia* collected in the field during one year, only 0·73 per cent. were found parasitised, the highest degree of parasitism occurring during the months of January to March. The proportion of parasitised *Sesamia* pupae to *Proceras* was 4 to 2.

This parasite probably has many hosts in the field, as shown by the experiment recorded in Table XIII, but the only one recorded, apart from *Sesamia* and *Proceras* was *Simplicia inarcualis* Gn.


0·5 mm
a
0·5 mm
b
1 mm
d
k
0·05 mm
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s
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m
o
h
0·25 mm
n
p
0·025 mm
t
u
1 mm

Fig. 7.—*Xanthopimpla citrina* (Hlmgr.) : *a*, egg ; *b*, first-stage larva with tracheal system ; *c*, head capsule ; *d*, second-stage larva with tracheal system ; *e*, head capsule ; *e′*, mouth-parts showing position of mandibles ; *f*, head capsule, third-stage larva ; *g*, fourth-stage larva ; *h*, cuticular structure ; *i*, tracheal system, ventral view ; *j*, tracheal system, lateral view ; *k*, spiracle ; *l*, head capsule ; *m*, mandible, first-stage larva ; *n*, mandible, second-stage larva ; *o*, mandible, third-stage larva ; *p*, mandible, fourth-stage larva ; *q*, *r*, *s*, labral, labial and maxillary sensillae, respectively ; *t*, prepupa ; *u*, pupa.

Xanthopimpla citrina (Hlmgr.) (Hym., Ichneumonidae).

This species was described by Holmgren from specimens received from Mauritius. Its recorded hosts in Mauritius are *Sesamia vuteria, Proceras sacchariphagus* and *Nacoleia praeteritalis* (Moutia & Mamet, 1947). Its geographical distribution is unknown. Seyrig (1932) considers the genus *Xanthopimpla* to be of Ethiopian and Indo-Malayan origin. This author further suggests that all the forms known (*viz. dorsigera, stulta, impolluta* and *luteola*) and previously recorded as different species of *Xanthopimpla* should be grouped under the priority name *citrina* as *Chrysopimpla citrina* Hlmgr.

Egg (fig. 7 *a*).

White, elongate-oval, translucent and shiny. Its chorion is smooth and unsculptured. The egg measures 1·2 mm. in length and 0·24 mm. at its widest part. Before hatching it becomes pale-yellow and increases slightly in size.

First-stage larva (fig. 7 *b*).

On hatching, white, transparent and clearly segmented. The head capsule is at first white, transparent and unsclerotised but its cuticle hardens during the first 24 hours and acquires an amber coloration. Its structure is as shown in fig. 7 *c* ; it consists of three plates, one dorsal and a pair of lateral ones which do not meet ventrally. The mandibles, fig. 7 *m*, measure 0·18 mm. in length and 0·08 mm. in width at the base ; they are long, sickle-shaped, without serrations and light-brown in colour. The antennae are vestigial. The cuticle of the body is shiny ; viewed under high magnification it is seen to bear numerous stout, conical setae all over each segment. The tracheal system consists of two main lateral trunks connected anteriorly by a dorsal commissure situated at the base of the head capsule, and posteriorly by a transverse ventral commissure situated at about the twelfth body segment. Lateral tracheal commissures are present in the second and third thoracic segments. Secondary trunks connected with one another emerge on each side of the main lateral trunks from the first to the eighth abdominal segments. There are also secondary trunks terminating in the caudal region. Spiracles are absent. At this stage the larva measures about 3·2 mm. in length and 0·83 mm. at its greatest width ; its head capsule measures 0·37 mm. in length and 0·35 mm. in width.

Second-stage larva (fig. 7 *d*).

White and transparent except for the gut. The head capsule (fig. 7 *e*) is unsclerotised and the mouth parts (fig. 7 *e'*) bear slightly sclerotised mandibles (fig. 7 *m*) which are simple, smooth and brown at the tip ; the base of the mandible is white and measures 0·13 mm. The 13 body segments are well defined, the last one being short and tail-like. The cuticle is very shiny and bears very short spines which are more numerous at the posterior end of the body. The tracheal system is similar to that found in the first-stage larva. Spiracles are absent. Length of second-stage larva, 5·06 mm., width, 1·06 mm. ; length of head capsule, 0·31 mm., width 0·35 mm.

Third-stage larva (fig. 7 *f*).

Cylindrical, creamy-white and opaque. The head, which remains unsclerotised, is more ventral in position. The mandibles (fig. 7 *o*) are nearly the same size as in the preceding stage. The integument is spinose over the whole body. This stage differs from the preceding one in a marked increase in size and in the presence of spiracles, distributed as in the succeeding stage described below. Length of third-stage larva, 6·38 mm., width, 2·38 mm. ; the head capsule measures 0·58 mm. in length and 0·62 mm. in width.

Fourth-stage larva (fig. 7 *g*).

Cigar-shaped and buff to light-brown in colour. The head is hemispherical in shape, slightly inclined ventrally and unsclerotised; the mouth-parts are sclerotised, the mandibles (fig. 7 *p*) having dark-brown tips. A dorsal hump extends longitudinally on each segment from 4 to 11, the humps being more pronounced on segments 6 to 11; the middle of the body dorsally is slightly depressed. Lateral hypopleural lobes are present on segments 2 to 11. The cuticle is shiny and translucent and bears small conical papillae as shown in fig. 7 *h*. These papillae are regularly distributed on all the body segments and are stouter on the lateral lobes. No setae were detected, even under high magnification. The tracheal system is shown in fig. 7 *i*, *j*. The dorsal tracheae leave the lateral trunks anterior to the spiracles and do not fuse with one another; the ventral tracheae leave the lateral trunks a little behind the spiracles and divide into two main branches one of which fuses with the corresponding branch of the other main tracheal trunk forming a ventral commissure. These commissures are found on the fourth to the eleventh segments. Nine pairs of spiracles are present; the first pair occurs near the posterior margin of the first thoracic segment and is more developed than the others, which are situated near the anterior margins of the third thoracic and the first seven abdominal segments. A spiracle is shown in fig. 7 *k*. The atrium is large, spherical and 0·05 mm. in diameter; its external opening measures 0·04 mm. in diameter. The inner wall of the atrium is lined with short processes projecting towards the centre of the structure. The stalk of the spiracle is barrel-shaped and is divided into partitions by five or six plates. No trace of spiracles was observed on the second thoracic segment. The mouth-parts are as shown in fig. 7 *l*. The mandibles (fig. 7 *p*) are pointed and smooth and measure 0·20 mm. in length and 0·17 mm. in width. The hypopharynx is armed with very sharp teeth. The labral, labial and maxillary sensillae are as shown in fig. 7 *q*, *r*, *s*. The mature larva varies considerably in length according to the size of the host pupa. The maximum length recorded was 17·6 mm. and the maximum width 11·0 mm., the corresponding minimum dimensions being 15·5 mm. and 4·0 mm.

Prepupa (fig. 7 *t*).

Pupa (fig. 7 *u*).

Pale yellowish-white and darkens with age to the colour of the adult. The eyes are light reddish-brown. The pupa measures 13·9 mm. in length and 2·9 mm. in width at the thorax.

Life-history.

The adults are active insects and seldom motionless. They are attracted to light. They copulate readily as soon as they have emerged; copulation usually lasts only a few seconds, but occasionally continues for two to three minutes. In the field, it takes place between 9 and 11 a.m. The males are generally on the wing about an hour earlier than the females. Adults in breeding jars 12 ins. and 5 ins. in diameter copulate every two or three days throughout their life. The preoviposition period in summer is 10–12 days. The number of ovarioles per female is from 6 to 12 and the number of mature eggs present at a time varies from 5 to 14.

The female is frequently seen in the field flying to and fro, and searching for a host pupa by thrusting the ovipositor in the frass at the entrance of a borer tunnel or in folded cane trash harbouring a pupa. When a pupa has been detected, oviposition is effected with several jerking movements of the abdomen. Characteristic movements of the wings and accelerated vibration of the antennae also accompany oviposition, which generally lasts from 1 to 2 minutes. The female, after withdrawing the ovipositor, feeds upon the body fluid which oozes from the puncture. Sometimes two or three punctures are made before the deposition of an egg, and each time the body liquid is greedily sucked by the female. The ovipositor does not appear to be inserted into any particular region of the host pupa. Only one egg per pupa was found in pupae parasitised in the field, but in the laboratory a pupa may be parasitised three to five times, the female showing no reluctance to oviposit again in the same pupa. As many as five larvae may hatch in a superparasitised pupa, but only one reaches the final instar, the others dying after the first or second moult. Host pupae of all ages are acceptable to the adult, but it is only in pupae between one and six days old that the parasite can complete its development. One fertilised female was provided each day with host pupae and kept under observation in a breeding jar with food. When it attacked a pupa this was removed and retained to see if parasitism had occurred. It was found that a total of 22 eggs were laid by this female during its life of 25 days.

The duration of adult life was found to be about 30 days for females and 20 days for males, when the insects were kept in breeding jars and amply supplied with food, at a mean temperature of 23·5°C. ; the maximum longevity recorded was 45 days. Under the same conditions but without food, adults lived for 8–10 days. The sex ratio of adults bred in the laboratory was three males to two females, in 75 individuals.

Parthenogenesis.

This occurred with some individuals, the offspring being male. The life-cycle is relatively short in summer, the total period of development being on the average 14 days (mean laboratory temperature, 24·5°C.) ; the incubation period and the first three larval stages each last one day and the fourth stage lasts two days. There is a prepupal period of one day, at the end of which a meconium is expelled and the pupa is formed. Eight days later, the adult emerges through an opercular opening which it makes at the anterior end of the host pupa. In winter, the life-cycle is about 25 days, the incubation period is increased by one day, and the larval and pupal periods are each about 12 days. The size of the adult is closely related to that of the host pupa ; individuals half the average size were very often obtained.

Natural parasitism.

In the field, adults are found in fairly large numbers in the uplands from January to April, coinciding with *Sesamia* outbreaks, and in the lowlands from July to October when *Proceras* is numerous in cane fields. This parasite, though very commonly found in cane fields heavily infested with *Olethreutes schistaceana*, was never recorded from field-collected pupae of this borer, despite the fact that in the laboratory, parasitism of these pupae readily occurred. The degree of parasitism in field-collected pupae of *Proceras* and *Sesamia* is shown in Table XVI.

TABLE XVI

Parasitism by *Xanthopimpla citrina* on *Sesamia* and *Proceras.*

Months	*Sesamia*			*Proceras*		
	No. of pupae collected	No. of pupae parasitised	Per cent. parasitism	No. of pupae collected	No. of pupae parasitised	Per cent. parasitism
January–February ...	83	4	4·8	28	1	3·5
March–April	30	1	3·3	17	1	5·8
May–June	46	1	2·1	32	1	3·1
July–August	32	1	3·1	125	8	6·4
September–October ...	97	2	2·1	120	3	2·5
November–December ...	49	1	2·0	146	3	2·1
Total	337	10	—	468	17	—
Mean percentage parasitism (from totals above) :			2·9			3·6

From the above table it appears that there are two peaks of parasitism, in January–February and July–August. These figures corroborate field observations.

Xanthopimpla stemmator (Thunb.) (Hym., Ichneumonidae).

This species was introduced from Ceylon into Mauritius in 1939 (Vinson, 1942). Its known distribution is : India, Formosa, Java, Batyan, Kei Islands. Its hosts in India are *Chilo zonellus* (Swinh.) and *Plusia orichalcea* (F.), and in Formosa, *Pyrausta nubilalis* (Hb.), *Eucosma schistaceana* (Sn.), *Chilo infuscatellus* Sn., *Diatraea venosata* (Walk.), *Omphisa illisalis* (Walk.), *Metanastria punctata* (Walk.), *Scirpophaga nivella* (F.) and *Sesamia inferens* (Walk.) (Sonan, 1929 ; Cartwright, 1933 ; Takano, 1934). In Ceylon, it is reported on *Chilo zonellus* (Vinson, 1942). In Java, Diakonoff (1948) reports that this species "appeared in about 5% of borers in *Saccharum spontaneum* but was not found in borers in cane fields". In Mauritius, it has been bred from *Sesamia vuteria* (Stoll.), *Proceras sacchariphagus* Boj. (Moutia & Mamet, 1947) and from *Argyroploce rhynchias* (Meyr.) during this work.

TABLE XVII.

Parasitism by *Xanthopimpla stemmator* on *Sesamia* and *Proceras.*

Months	*Sesamia*			*Proceras*		
	No. of pupae collected	No. of pupae parasitised	Per cent. parasitism	No. of pupae collected	No. of pupae parasitised	Per cent. parasitism
January–February ...	83	1	1·2	28	1	3·5
March–April	30	2	6·6	17	0	0
May–June	46	1	2·1	32	1	3·1
July–August	32	1	3·1	125	6	4·8
September–October ...	97	1	1·0	120	3	2·5
November–December ...	49	0	0	146	4	2·7
Total	337	6	—	468	15	—
Mean percentage parasitism (from totals above) :			1·8			3·2

Examination of the early stages failed to reveal any differences between this species and *X. citrina*. These two species are also very similar biologically. In their life-cycles, there is a difference in the durations of the pupal periods. Hence the total life-cycle in summer at 24·5°C. was found to average 17 days for *X. stemmator* and 14 days for *X. citrina*. In winter, at a mean temperature of 18·5°C., the difference is more apparent, the complete life-cycle of *X. stemmator* covering 31 days and that of *X. citrina* 25 days.

The number of ovarioles per female is from four to six pairs and the number of mature eggs present in them at any one time rarely exceeds eight. The duration of life of females kept in breeding jars and fed with raisins reached a maximum of 67 days in summer, the mean being 35 days. In winter, some females remained alive for 90 days under the same conditions. The sex ratio, female to male, is 1 : 1·7.

The parasitism of field-collected host pupae is shown in Table XVII.

Discussion.

Since 1938, attempts have been made to establish in Mauritius parasites of cane moth-borers from other countries. The species which have been introduced are :

Trichogramma evanescens Westw., *Bracon albolineatus* Cam., *Xanthopimpla stemmator* (Thunb.) (Jepson, 1941 ; Vinson, 1942), *Euvipio rufa* Szépl. (Moutia, 1948), *Paratheresia claripalpis* (Wulp), *Lixophaga diatraeae* (Tns.) and *Metagonistylum minense*, Tns. (Moutia, *loc. cit.* ; Williams, 1949, 1951a).

Only the introduction of *X. stemmator* has so far proved successful. *B. albolineatus* was reared once in 1948 from a *Sesamia* larva attacking rice (Williams, 1949), and the senior author has sometimes found it on the wing in rice fields, but although it has clearly become established, its introduction cannot be considered as having attained its object.

Experimentation with other parasites is proceeding ; these are *Agathis stigmatera* (Cress.) and *Telenomus alecto* (Crwf.) from Trinidad.

Parasites of the three species of moth-borers of sugar-cane in Mauritius comprise ten species, one of which is a hyperparasite. Table XVIII summarises the data collected during the last 2 years and gives an idea of the status of these parasites. It was found during the present survey that the relative importance of the various species may vary considerably from one year to another and sometimes from one parasite generation to another.

These data show that the nine species of primary parasites exert no substantial check on the multiplication of the borers. The low degree of parasitism is indicated by the persistence of permanent foci of infestation.

It is to be concluded that the introduction of parasites from other countries should be continued in the interests of the cane-growing community of Mauritius.

TABLE XVIII.

Parasitism of *Sesamia vuteria, Proceras sacchariphagus* and *Olethreutes schistaceana.*

Parasite species	Estimated annual percentage parasitism of		
	S. vuteria	*P. sacchariphagus*	*O. schistaceana*
EGG PARASITES.			
Trichogramma ? australicum	*	5·9	*
Trichogramma sp.	*	Nil	{Max. 64·7, Oct.-Nov. Min. 10·0, June-July}
Platytelenomus ? hylas	6·5	Nil	Nil
LARVAL PARASITES.			
Apanteles flavipes	Nil	7·5	Nil
Calliceras ? fijiensis	(Secondary through *Apanteles flavipes*)		
Enicospilus sp.	3·4	Nil	Nil
Nematodes (*Mermis* sp.)	*	*	Nil
PUPAL PARASITES.			
Tetrastichus sp. near *atriclavus*	0·4	0·2	Nil
Xanthopimpla citrina	2·9	3·6	Nil
Xanthopimpla stemmator	1·8	3·2	Nil

* Negligible.

Summary.

There are three moth-borers of sugar-cane in Mauritius, *Proceras sacchariphagus* Boj. (Crambid.), *Sesamia vuteria* (Stoll) (Agrotid.) and *Olethreutes schistaceana* (Snell.) (Olethreutid.).

The eggs of all three are parasitised by *Trichogramma* sp. ? *australicum* Gir., while a second undetermined species of *Trichogramma* parasitises the eggs of *Sesamia* and *Olethreutes*. *Sesamia* eggs are also parasitised by a Scelionid, *Platytelenomus* sp. ? *hylas* Nixon.

The larvae of *Sesamia* are parasitised by an Ichneumonid, *Enicospilus* sp., and those of *Proceras* by a Braconid, *Apanteles flavipes* (Cam.). No parasite is recorded from larvae of *Olethreutes schistaceana.*

The pupae of *Sesamia* and *Proceras* are parasitised by a Eulophid, *Tetrastichus* sp. near *atriclavus* Waterst. and by two Ichneumonids, *Xanthopimpla citrina* (Hlmgr.) and *Xanthopimpla stemmator* (Thunb.). No pupal parasite of *Olethreutes* is recorded, but field and laboratory observations suggest that both species of *Xanthopimpla* may parasitise it.

Apanteles flavipes is hyperparasitised by *Calliceras* sp. ? *fijiensis* Ferrière, but not to any considerable extent.

Hosts of the egg parasites, other than the moth-borers, are recorded. For *T. australicum*, these are *Achaea trapezoides* (Gn.), *Autographa chalcytes* (Esp.) and *Melanitis leda* (L.). The first two are also hosts of the undetermined *Trichogramma* sp. The only other host recorded for *Platytelenomus* sp. ? *hylas* is *Autographa chalcytes.* Other hosts of the pupal parasites are *Simplicia inarcualis* Gn. for *Tetrastichus* sp. near *atriclavus*, *Argyroploce rhynchias* (Meyr.) for *Xanthopimpla citrina* and *Nacoleia praeteritalis* Walk. for *Xanthopimpla stemmator.*

The activity of these parasites in the field has been studied.

Descriptions of the developmental stages and of the biology of the eight species of primary parasites and the one hyperparasite are given.

The relative economic value of each species of parasite in the control of moth-borers in Mauritius is discussed.

Acknowledgements.

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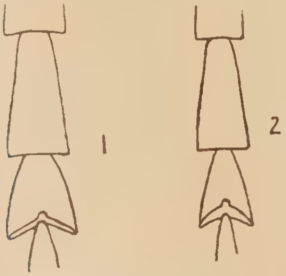
ON SOME BRITISH SPECIES OF *ICHNEUMON* AND *ALOMYIA* (HYM., ICHNEUMONIDAE).

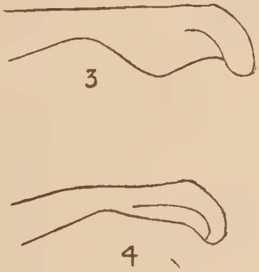
By J. F. PERKINS.

(*British Museum, Natural History*).

Ichneumon suspiciosus Wesmael (1844) and **I. septentrionalis** Holmgren (1864).

There has been considerable confusion in the determination of *I. suspiciosus* Wesmael. In fact, in Wesmael's series of this species in the Brussels Museum, the two species here differentiated were both represented. However, only one of these species agreed completely with his original description, and unfortunately this is not the species determined as *suspiciosus* by Thomson and by Roman. This latter form I regard as being a subspecies of *I. septentrionalis* Holmgren.





Figs. 1–2.—Hind tarsus of ♀: (1) *I. septentrionalis* (2) *I. suspiciosus.*
Figs. 3–4.—Apex of penis valves, lateral: (3) *Alomyia debellator* (4) *A. semiflava.*

The two species differ as follows :—

septentrionalis ♀	*suspiciosus* ♀
Hind coxa beneath, with the inner margin raised into a low ridge, and this area finely and very closely punctate.	Hind coxa with the inner margin unraised and less closely and less finely punctate along this margin.
Tarsi with the segments relatively broader (fig. 1).	Tarsi with the segments relatively more elongate (fig. 2).
Segments of posterior tarsi entirely testaceous, or, of the hind tarsus, very weakly infuscate apically.	Segments of posterior tarsi at least in considerable part, conspicuously infuscate.
septentrionalis scelestus ♂	*suspiciosus* ♂
Face with at least a large black mark above the clypeus, varying to black with only the orbits yellow ; clypeus most usually in large part black.	Face entirely yellow ; clypeus yellow, sometimes narrowly fuscous apically.
Flagellum entirely black ; scape rather narrowly yellow beneath.	Flagellum broadly testaceous beneath ; scape broadly yellow beneath.
Mesonotum more shining, laterally with only the faintest trace of microsculpture between the smaller and less deeply impressed punctures ; mesopleurum more sparsely punctate.	Mesonotum rather dull, laterally in part with distinct microsculpture between the larger and deeper punctures ; mesopleurum closely punctate with the interspaces tending to run into striae.
Scutellum little convex.	Scutellum distinctly convex.
Abdomen usually broader with the third tergite a little transverse.	Abdomen narrower with the third tergite quadrate.
Hind tarsus yellow, sometimes with the apical segments testaceous.	Hind tarsus testaceous with at least the apical segments more or less infuscate.
Abdomen with tergites 2 and 3 yellow, most usually marked with red.	Abdomen with tergites 2 and 3 red, marked with yellow.

The males of both species have small tyloidae on flagellar segments 6/7–15/16, and the pronotal collar conspicuously yellow marked.

I. septentrionalis septentrionalis Holmgren.

I have seen no male of this subspecies. The female has the femora and tibiae red, the tibiae more or less marked with yellow towards the base. Recorded by Holmgren from Sweden: Dalecarlia; South Lapland, Tärna; Westerbotten, Tafvelsjö; Jemtland, Åreskutan. Norway: Dovrefjeld. Thomson gives Lapland and Norrland. I have seen a single female from Dalecarlia (Holmgren Collection) through the kindness of Dr. R. Malaise and Mr. G. J. Kerrich.

I. septentrionalis scelestus subsp. n. ♀

Differs from the above in having: Front femur conspicuously marked with black; middle femur black except for base and apex, hind femur black, very narrowly red basally; hind tibia infuscate basally, broadly black apically.

HOLOTYPE. England: Sussex, nr. Worthing, 29.i.1923, under elm bark (*F. Collins*).

PARATYPES. England: 9 ♀, Desvignes Coll; 1 ♀, West Suffolk, 1928, (*P. Harwood*); 1 ♀, Gloucestershire, Forest of Dean, 18.v.1945 (*C. T. Gimingham*); 1 ♀, North Yorkshire, Teesdale, 1,000–1,200 ft, 31.v. to 7.vi.1939 (*J. E. & R. B. Benson*).

Sweden: 1 ♀, Stockholm (*Boheman*).

Switzerland: 1 ♀, Wengen 6.vi.1939 (*G. M. Spooner*).

Czechoslovakia: 1 ♀, Bohemia, Chodau, 25.v.07 (*Stein*).

I. suspiciosus Wesmael.

Of this species, which is similarly coloured to *I. septentrionalis scelestus*, I have seen material from England (many specimens, including 1 ♂ 1 ♀ ex *Hepialus lupulinus* (L.) (*Cameron*)); Belgium (Coll. Wesmael, including lectotype); Switzerland, 1 ♀, Zurich, 5.viii., Buchecher Coll. *Ichneumon suspiciosus* is more closely related to *I. albiger* Wesmael, in the sculpture of the coxae and the relative length of the tarsal segments. Superficially, it can be distinguished at once from that species in having the ivory spot on the fifth tergite broader than that on the sixth; in *albiger* (syn. *tempestivus* Holmgren, the aberration with the hind tibia marked with yellow), the fifth tergite is usually entirely black and at most with a very small, ivory, apical spot. In addition, *suspiciosus* has the scutellum narrower, the second and third tergites more closely punctate, the malar space a little longer and the cheek less buccate than in *albiger*. In *suspiciosus*, the white band on the antenna is on segments 9/10–16/17, usually on 10–16; in *albiger*, on 9/10–14. *I. suspiciosus* Wesmael is the species which has, for the most part, been recorded under this name from Britain. All the specimens in the Hancock Collection under this name, taken hibernating in grass tufts and from under bark, are of this species.

Alomyia debellator (F.) (1775) and **A. semiflavus** Stephens (1835).

Two species have been confused in recent years under *Alomyia debellator* (F.), *semiflavus* Stephens (=*A. debellator* var. *minor* Ulbricht, **syn. nov.**) having been regarded as a synonym of that species.

debellator (F.)	*semiflavus* Stephens
v.–ix.	viii.–x.
♀♂ Transverse median of hind wings most usually angled at the lower one-third.	♀♂ Transverse median of hind wings most usually angled at the lower one-quarter.
♀ Second tergite with the groove surrounding the spiracle about as far from the lateral margin as its (transverse) diameter.	♀ Second tergite with the groove surrounding the spiracle at least 1⅔ times as far from the lateral margin as its diameter.
Flagellum most usually with segment 1–10/11 pale testaceous the remaining segments fuscous (sometimes in part marked with testaceous) or sometimes the whole flagellum in large part conspicuously infuscate.	Flagellum usually with segments 1–3/4 fuscous, 4/5–13/14 very pale testaceous or yellow (British specimens—the single ♀ from Germany has segment 3 also marked with yellow).
♂ Second tergite with the spiracle conspicuously closer to the lateral margin than its diameter.	♂ Second tergite with the spiracle at least as far from the lateral margin as its diameter.
Tergites 2–4 testaceous, 4 black apically, in dark specimens the black appearing as a broad longitudinal bar in the middle of the segment—varying to completely black.	Apex of tergite 1, and tergites 2–4 yellow, with a pair of testaceous spots just behind the middle, tergite 4 often with a triangular black, apical mark ; varying through the testaceous spots becoming black and the fourth segment much suffused to the abdomen completely infuscate.
Hind tibia testaceous, frequently infuscate apically, varying to entirely black.	Hind tibia pale yellow, even in the darkest specimens only narrowly infuscate apically.
Stigma darker with the outer hind margin always infuscate.	Stigma paler with the outer hind margin darker only in strongly infuscate specimens.
Penis valves with a strong, sub-apical expansion (fig. 3).	Penis valves with no sub-apical expansion (fig. 4).

I have seen the following material in the British Museum Collection :—

Alomyia debellator 98♂, 23♀	England, Scotland, Ireland, France, Germany, Switzerland, Poland and Czechoslovakia.
Alomyia semiflavus 65♂, 12♀	England and Germany.

G. Heinrich (1949, Mitt. Münch. ent. Ges., **35–39** (1945–1949) p. 74) has described a third species of *Alomyia*—*A. pygmaea*, from Bavaria.

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THE SHINYANGA GAME DESTRUCTION EXPERIMENT.

By W. H. Potts, M.A., and C. H. N. Jackson, D.Sc.

East African Tsetse and Trypanosomiasis Research and Reclamation Organisation, Tanganyika.

The Shinyanga Game Destruction Experiment resulted from strong requests from the East African Standing Committee for Tsetse and Trypanosomiasis Research at its first and second meetings (June 1943 and February 1944). It took the place of an earlier experiment planned by the late C. F. M. Swynnerton and started as a part of the scheme of Tsetse Research financed by a grant from the Colonial Development and Welfare Fund in 1938, but closed down at the outbreak of war in 1939.

As well as reporting the results of this experiment we have allowed ourselves some expressions of opinion on the general applicability of game destruction. These opinions are entirely our own and do not necessarily reflect those of our organisation.

The primary object was to determine whether the common savanna species of tsetse, *Glossina morsitans* Westw., *G. swynnertoni* Aust. and *G. pallidipes* Aust., could be eradicated by the destruction of the hoofed game animals under conditions prevailing in Tanganyika, and if so over what period and at what cost. In part of Southern Rhodesia *G. morsitans* has already been eradicated in this way.

It was also desired to discover whether, if the larger big game animals were destroyed, the flies could maintain themselves on small antelopes and pigs, which therefore were to be spared until the result of destroying the larger species was known. This object was unfortunately defeated completely, because it proved impossible to prevent the shooters from killing the smaller species, though as they naturally did not declare them we do not know how many were shot. From the reduction in numbers of small animals recorded, as seen by the fly-boys, it seems that at least three-quarters of them disappeared.

A second subsidiary object was the study of a hungry tsetse community. Although it is very well known what constitutes a hungry fly, a hungry community is not of course made up entirely of hungry individuals at any one time, and we wanted to know whether there were symptoms by which we might recognise hungry communities in the field. As will appear below, with the slow rate of extermination of flies that was achieved, the signs of hunger, though definite, were too slight to be generally useful.

Site.

The area had to be surrounded by a barrier to both the fly and the game. This barrier could be natural or artificial, but as the area would need to be large enough to support a sufficient variety of animals it was out of the question to use one which would require a mainly artificial barrier. The choice therefore fell on the area (blocks 13 to 16) illustrated on the sketch map. It is isolated from invading flies on all sides by wide stretches of treeless country, and nearly isolated from invading game animals on the east, south and west by settlements. On the north however it borders on a grassy plain grazed by game and cattle ; it was hoped to keep the animals out by shooting, but eventually a game fence 50 miles long had to be erected on that side. The experimental area comprised some 600 sq. m. of uninhabited bush country, and was exceptional in containing all three species of tsetse named above. It had also the great advantage of being near both to our laboratory at Old Shinyanga an to untouched areas of tsetse-infested bush which could be used as controls. It was the only area known to us which combined all these advantages.

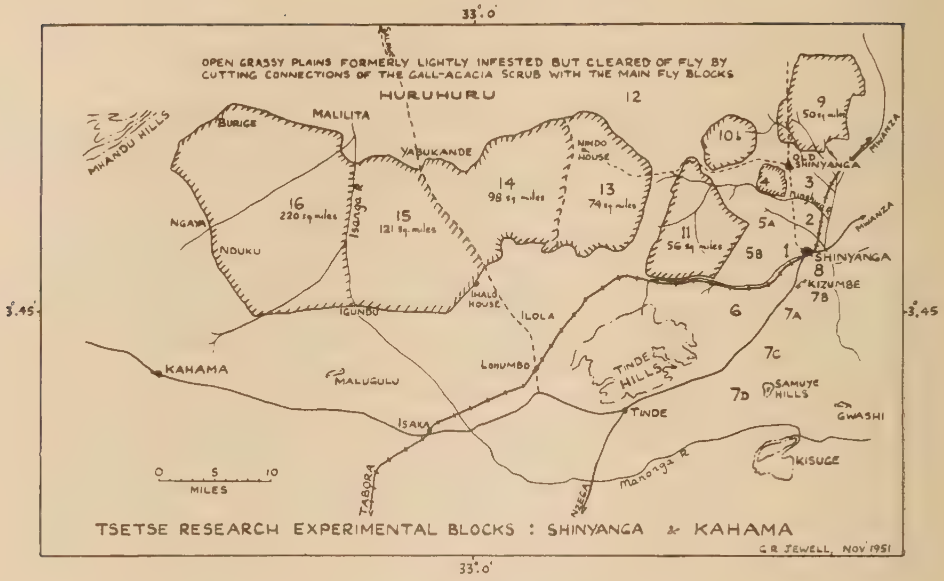
33°.0'
OPEN GRASSY PLAINS FORMERLY LIGHTLY INFESTED BUT CLEARED OF FLY BY
CUTTING CONNECTIONS OF THE GALL-ACACIA SCRUB WITH THE MAIN FLY BLOCKS
HURUHURU
12
MHANDU HILLS
BURIGE
MALILITA
YABUKANDE
NINDO HOUSE
9
50 sq miles
10b
MWANZA
OLD SHINYANGA
4
3
Ningh...
16
220 sq miles
Isanga R
15
121 sq. miles
14
98 sq miles
13
74 sq miles
11
56 sq miles
5A
2
MWANZA
NGAYA
NDUKU
5B
1
SHINYANGA
8
KIZUMBE
7B
3°.45'
IGUNDU
IHALO HOUSE
ILOLA
6
7A
3°.45
KAHAMA
MALUGULU
LOHUMBO
TINDE HILLS
7C
7D
SAMUYE HILLS
ISAKA
TINDE
GWASHI
0 5 10
MILES
TABORA
Manonga R
KISUGE
NZEGA
TSETSE RESEARCH EXPERIMENTAL BLOCKS : SHINYANGA & KAHAMA
G R JEWELL, NOV 1951
33°.0'

Fig. 1.

The Vegetation.

The vegetation in the eastern portion (blocks 13 and 14) consisted of *Acacia-Commiphora* thornbush communities, intersected by grassland with gall-acacias, on cracking clay soils, and interspersed with blocks of dense thicket of *Grewia* and *Combretum trothae*. The middle of the area (block 15) has less thicket and a greater proportion of open grassland, and the southern part of the western portion (block 16) was distinguished by the presence of *Brachystegia-Isoberlinia* broad-leaved deciduous woodland on granitic soils. The grassy plains to the north of the experimental area resembled its grasslands in having much gall-acacia but were of course more extensive.

The Game.

Large animals common throughout the area were giraffe, roan antelope, Bohor reedbuck, eland, and impala : wildebeest, topi, Thomson's gazelle and zebra wandered in from the northern plains. Rhinoceros were widespread. Common small animals, which were shot as a result of the uncontrollable hunting instincts of the African shooters, were duiker, steinbuck, oribi, dikdik, wart-hog and bush-pig.

In the west there were also greater kudu and bushbuck, with a few Lichtenstein's hartebeest, sable antelope, southern reedbuck and occasional buffalo. Three lesser kudu, one situtunga, a klipspringer and a hippopotamus were shot. A few elephant appeared for short periods during 1950 but were unmolested. Finally, ostrich entered the area from the plains ; these had to be shot, for being large ground animals they could not be neglected as a source of food for starving tsetse.

Lion and leopard were shot or trapped whenever possible in view of the possible danger to man and cattle.

Game Animals known to have been shot.

Zebra, *Equus burchellii* Gray	339
Rhinoceros, *Diceros bicornis* L.	15
Hippopotamus, *Hippopotamus amphibius* L.	1
Giraffe, *Giraffa camelopardalis* L.	641
Buffalo, *Syncerus caffer* Sparrman	3
Roan Antelope, *Hippotragus equinus* Desmarest	393
Sable Antelope, *Hippotragus niger* Harris	3
Topi, *Damaliscus korrigum* Ogilby	654
Hartebeest, *Alcelaphus lichtensteinii* Peters	36
Wildebeest, *Gorgon taurinus* Burchell	218
Bohor Reedbuck, *Redunca redunca* Pallas	1,450
Southern Reedbuck, *Redunca arundinum* Boddaert	34
Eland, *Taurotragus oryx* Pallas	891
Greater Kudu, *Strepsiceros strepsiceros* Pallas	88
Lesser Kudu, *Strepsiceros imberbis* Blyth	3
Situtunga, *Limnotragus spekei* P. L. Sclater	1
Bushbuck, *Tragelaphus scriptus* Pallas	60
Impala, *Aepyceros melampus* Lichtenstein	1,217
Thomson's Gazelle, *Gazella thomsonii* Günther	2,038
Ostrich, *Struthio camelus* L.	469

Small Animals believed shot against Orders.

Wart-hog, *Phacochoerus aethiopicus* Pallas
Bush-pig, *Potamochoerus porcus* L.
Common Duiker, *Sylvicapra grimmia* L.
Klipspringer, *Oreotragus oreotragus* Zimmermann
Steinbuck, *Raphicerus campestris* Thunberg
Oribi, *Ourebia ourebi* Zimmermann
Dikdik, *Rhynchotragus kirkii* Günther

The animals can be divided into bush game and plains game. The latter include zebra, wildebeest, topi, Thomson's gazelle and ostrich. These resided mainly outside the tsetse-fly area and entered it only from time to time, but especially at the break of the rains, and later when the grass plains to the north became very wet. Of those classed as bush game, the eland are often seen on the plains and are great wanderers, and they too usually showed marked increase in the area about the break of the rains; at other times most would be elsewhere. The impala are common on the plains especially in the gall-acacias, as well as in the bush; these and the reedbuck were shot more by the hunters later on when larger animals were scarce. Many of them would doubtless have been born and reared during the shooting and were therefore not in the area at the start; these for census purposes would to some extent cancel out the large number undoubtedly surviving at the end. Kudu and bushbuck are very difficult to exterminate, and many bushbuck certainly survived.

In our opinion, the bulk of the giraffe, roan antelope, Bohor reedbuck, greater kudu, bushbuck and rhinoceros shot in the area were either present there at the start or (in a few cases) were born and reared during the progress of the shooting. We consider that making due allowance for movements in and out of the area it would be reasonable to suppose that when the shooting began it might have contained 500 giraffe, 300 roan antelope, 800 Bohor reedbuck, 70 or more greater kudu, 100 bushbuck and 12 rhinoceros. In addition, there might have been on the average 200 eland, 500 impala and perhaps a quarter of the plains game eventually shot, that is to say 50 wildebeest, 150 topi, 500 Thomson's gazelle, 80 zebra and 100 ostrich. The other species shot are too casual visitors to mention. In addition there was, however, a very large population of duiker, dikdik, oribi, steinbuck, wart-hog and bush-pig which we think must have been at least as numerous as all the other animals put together. In this conclusion we are supported by the Annual Reports of the Southern Rhodesian shooting, where, although there are no dikdik, about half the kill is small antelopes and pigs.

It may seem surprising that with a total kill of over 8,000 in addition to a number remaining alive at the end of the shooting we should suggest an average population of little over 3,000 large animals in the area. The reason is that many of the animals killed would at any one time have been based on the open plains to the north, on the borders of which, in fact, much of the shooting took place before the game fence was put up ; and also at the break of the rains there is always a great seasonal incursion of eland and other animals. We thus conclude that the experimental area contained about 6,000 Ungulate animals of all species in its 600 sq. miles. There had always been, especially in the west, a great deal of shooting by Africans with muzzle-loaders. From extensive travels in Tanganyika and Northern Rhodesia we are able to say that the experimental area before our shooting began had a game density much like that of the bushed areas of these territories.

Our figure of ten animals per sq. mile is perhaps worth noting as illustrating the contrast between the numbers of game animals in protected and unprotected areas of Africa, displayed in the following table.

	Large animals per sq. mile	Total per sq. mile	Notes
	Protected		
Mkuzi	37	128	Shot to near extermination.
Umfolozi	82	795	,, ,, ,,
Kagera	40	—	Estimated total present.
	Unprotected		
Southern Rhodesia	1	2	Shot per year.
Northern Rhodesia	—	4	Shot in 2 years.
Ngamiland	—	1	,, ,, ,,
Shinyanga	5½	10	Estimated total present.
	14	—	Shot in 5 years.

In the case of Kagera and Shinyanga at least, " large animals " means impala size and upwards.

The Zululand figures, and those from Northern Rhodesia and Ngamiland are based on the figures given by Buxton (1948) ; those from Southern Rhodesia are taken from its annual reports and those from the Belgian Congo are estimates by M. Verhulst, warden of the Kagera National Park, as quoted by Mary Akeley (1951). The figures for Southern Rhodesia, based on the numbers annually killed, are obviously very much too low, because extermination was not achieved in 1 year. The Northern Rhodesian and Ngamiland figures also may be on the low side, for we do not know how nearly extermination was approached by the numbers of animals killed in the 2 years on which they are based. In the last area, anyhow, a large seasonal immigration of game is to be noted. But, approximate as it may be, this table does show two things ; that a very much lower density of game exists in the unprotected areas of Africa than in the protected ones and that the density of stocking in the former is so low that for a very long time to come the game existing on any land required for human occupation could be absorbed into the remaining areas without any danger of overstocking; there is, therefore, not complete justification for the contention that where African bush is needed for human use, the game must inevitably disappear ; it can move off into the unwanted areas. We do not deny that in some of the open grasslands there may be very heavy seasonal concentrations of game.

Our area probably contained about 20 grown lion from first to last, and perhaps 15 of these might have been there from the start. We destroyed a dozen. Leopard and hyaena would doubtless have been more numerous ; cheetah occurred chiefly on the plains to the north.

Organisation.

The first shooting was planned and started by Commander David Blunt, R.N., ex-Tanganyika Game Department, until ill-health caused his resignation in early October 1945 ; it was continued by Mr. S. J. Van Rensburg, and eventually by Mr. W. A. Hilton, who had worked for the Kenya Game Department as a Game and Vermin Control Officer, Mr. Van Rensburg continuing to assist. Mr. Hilton was established at Ihalo in the middle part of the area and Mr. Van Rensburg at Nindo in the east ; both are expert shots, and the former particularly experienced in the ways of the game animals.

The actual shooting was mainly done by Africans, at first 50, and later 100 as operations extended westwards ; as game became scarcer in the last 2 years shooters were again reduced. All underwent a course of training and were tested on targets before being sent out to shoot ; subsequently records of each hunter were watched so that any deterioration could be corrected by refresher courses and tests, and where necessary the hunter was replaced. The rifles were ·300 Remington, except for a period when their ammunition was unobtainable and ·303 rifles were used. For rhinoceros, ·404 were used.

The shooters lived in small camps, usually with two men in each, with additional labourers carrying water and drying the meat. These camps were used as bases, but the parties were mobile, and, carrying water with them, were able to sleep out on the trail of a wounded animal. Every effort was made to avoid the escape of wounded animals, though anyone with hunting experience in Africa will realise that it is not possible to avoid this entirely, however good a shot one may be. The shooters were given an incentive to follow any wounded beast to a kill, for payment above a low basic rate was by results ; the meat was turned into biltong for rations, and the hides properly dried and sold for conversion into leather.

Shooting started in the eastern portion of the area, Block 13 and part of Block 14 (see map), in July 1945, and was extended to the rest of Block 14 in March 1946, to Block 15 in May, and to the west of Block 16 in November of that year. In 1948 it was apparent that the shooting was not effectively preventing continued large-scale invasion by the plains game from the north, and a game fence 50 miles in length was erected and completed by September. This fence consisted of five strands of barbed wire to a height of 6 ft., supported on growing trees or cut poles. The fence was maintained by parties patrolling continuously, and though it was by no means fully effective it did immediately stop large-scale invasions by the plains game.

Observation.

Fly-boys collected samples of tsetse from fixed routes scattered through the area as well as from random catches. Similar routine catches were made in the control areas where the game were not being destroyed. The control for *G. morsitans* was 25 miles west of Kahama in *Brachystegia* woodland, and for *G. swynnertoni* and *G. pallidipes* in Block 9 near Old Shinyanga.

The samples of flies were examined monthly for comparison with the controls in respect of size and weight, age and fat content, and the proportion of females caught. Flies with recognisable blood were collected on special catches for determination of the percentage of nucleated bloods, assumed to be avian.

In addition, the fly-boys recorded the numbers of game animals that they saw during their work.

Effect on the Game.

The total number of animals recorded as shot was 8,554. The reduction in numbers is indicated by the following Table, with the important reservations that the number of shooters varied, that the full area was not included until November 1946, and that the shooters clearly paid more attention to the smaller impala and reedbuck as the larger species became less available to them, so that the numbers of larger species decline more sharply than the totals.

	1945 (half year)	1946	1947	1948	1949	1950
Bush game : larger animals—						
Rhinoceros	3	5	4	1	2	0
Hippopotamus	0	0	0	1	0	0
Giraffe	143	294	129	54	17	4
Buffalo	0	0	1	1	1	0
Roan	88	134	108	35	16	12
Sable	0	0	1	1	0	1
Hartebeest	0	0	15	14	7	0
Eland	47	276	301	185	61	21
Greater Kudu	0	6	31	31	15	5
Total	281	715	590	323	119	43
Bush game : smaller animals—						
Bohor Reedbuck	22	235	211	333	436	213
Southern Reedbuck	0	0	8	13	7	6
Lesser Kudu	0	0	1	2	0	0
Situtunga	0	0	0	0	1	0
Bushbuck	0	0	1	6	36	17
Impala	47	315	208	263	182	202
Total	69	550	429	617	662	438
Plains game—				Fence		
Zebra	36	183	99	15	1	5
Wildebeest	16	141	42	16	2	1
Topi	96	325	147	66	12	8
Thomson's Gazelle	42	660	697	383	70	186
Ostrich	2	148	165	85	54	15
Total	192	1,457	1,150	565	139	215
Full total	542	2,722	2,169	1,505	920	696

In addition to the actual reduction in numbers of the big animals recorded above, the game early became very wary and retiring and difficult to approach.

The effectiveness of the game fence is shown by the fact that up to September 1948, about half the animals shot were plains game (3,340 out of 6,695), but from October of that year the plains species formed only a fifth of the total (378 out of 1,859).

As already stated, there must have been, against our orders, a great but unreported destruction of duiker, dikdik, oribi, steinbuck, wart-hog and bush-pig. At least one klipspringer was also shot.

Effect on the Tsetse.

The best data are for *G. swynnertoni*, which was caught in the largest numbers both in the experimental area and in the control, Block 9. Shooting started in July 1945, and thereafter mean catches of non-teneral males along constant routes were :—

	1946	1947	1948	1949	1950	1951
Experiment	179·4	58·2	7·1	·5	·2	·0
Control	108·3	51·1	37·8	69·9	84·1	58·4

The control catches fell to 1,948 and then recovered in accordance with a well-known long-term cycle, but the catches in the experimental area fell heavily about April 1947, towards the end of the second rainy season after the start of the shooting, and then declined to nothing. (The figures quoted for the experimental area are from two fly rounds in the east of Block 13, where this species was most abundant and where the shooting began. Flies were however collected all over Blocks 13, 14 and 15, on other fly rounds and on random catches, and all these flies were used for the analysis of fat and other characters discussed below, but not for fly density comparisons since the catching sites varied from time to time.)

The fat content of non-teneral males fell in the experimental area, monthly means for the control averaging ·04 mg. higher in 1946, ·26 mg. in 1947 and ·42 mg. higher in 1948. Mean fat content in the control was about 2·2 mg.

The size of non-teneral males, measured by the length of the middle part of the fourth longitudinal vein (Jackson, 1946), fell compared with the control by ·00778 mm. (about five times its standard error) from 1946 to 1947, and again by ·00598 mm. (standard error ·00311) from 1947 to 1948. This effect had been expected, for the length of the vein, averaging in males of this species about 1·44 mm., is related to the weight of the larva at birth, and it is known that malnutrition in captivity causes larvae to be under-weight (Mellanby, 1937).

The non-fatty dry weight also fell in the experimental area compared with the control, the biggest drop (·15 mg.) occurring from 1946 to 1947. This weight is of course made up of two factors, the size of the fly and the amount of undigested dry matter remaining from its last meal.

Wings of all non-teneral male flies were examined to estimate age by wear on the trailing margin (Jackson, 1946), but there appeared to be no consistent difference between experiment and control. It is certainly to be supposed that expectation of life would be reduced with reduction of food animals ; on the other hand of course the birth rate might also fall.

A number of flies in Stage I of hunger (Jackson, 1933) collected on special searches were examined to determine the proportion of avian blood. The result was disappointing ; in 1947 and 1948 only one of 83 flies with recognisable blood showed nucleated cells.

The percentage of female flies in the catch of non-tenerals, which would be expected to rise with rising hunger, failed to do so perceptibly : the percentage was 15 in 1948, 18 in 1947 and 19 in 1948, compared with 11, 16 and 14 in the control.

The figures for *G. morsitans* will not bear such close analysis, because the control itself, though the best that could be found reasonably nearby, showed violent fluctuations in fat content of males, and a permanently high non-teneral female percentage (about 33 per cent.). The mean catch of non-teneral males in the control also fell more or less steadily from 51 in 1947 to 25 in 1951. A further difficulty was that in the south-west of the experimental area, where the regular fly rounds had been arranged before the shooting in 1946, the flies collapsed very quickly when operations began, from about 50 in September 1946 to five in the following April. Meanwhile a concentration not tapped by regular fly rounds persisted into 1949, and in the later stages provided most of the flies that were examined.

The only symptom of hunger shown by this species *vis-à-vis* the control was a fall in non-fatty dry weight of non-teneral males. In 1948, 75 non-teneral males per month were caught, 18 in 1949 and none at all in 1950 and 1951. Despite the 51 per cent. fall in numbers in the control from 1947 to 1951, there is no doubt that the extinction of this species in the experimental area can only be ascribed to the shooting.

The figures for *G. pallidipes* are even more unsatisfactory, mainly because in Shinyanga this species is so inactive in the presence of man or even of bait animals, and such flies as one finds have so little fat left that they can hardly be used for comparison between experiment and control. In the experimental area there was a sharp fall in numbers in September 1946, a little over a year from the start of the shooting in the main habitats of this species ; in 1950 only three males and two females were caught, and in 1951 a single female in June. This result however is viewed with considerable reserve, because though in Block 11 *G. pallidipes* maintained its numbers and even increased them from 1946 to 1951, in Blocks 4, 9 and 10 near Old Shinyanga numbers fell steadily until months passed without a single capture.

From November 1950 to October 1951 inclusive, 11 uninfected cattle were stationed in the experimental area at five widely separated points, Nindo, Yabukande, Izuka which lies between Igundu and Malilita, Burige and Mwaguhenga between Nduku and Igundu (see map). Every month these groups assembled at Ihalo for the taking of blood-slides, which were all negative. Finally blood-slides were taken on several consecutive days after the removal of the animals, again with negative results, and all the animals remained healthy throughout.

We conclude that *G. morsitans* and *G. swynnertoni* have been exterminated by the shooting of the game, and that *G. pallidipes* may or may not have been exterminated, but is certainly very rare.

It is interesting to note that this result has been achieved in spite of considerable incursions of cattle into the area during the late dry seasons throughout the experiment ; these had started during an interregnum in the early period of the war when the department had relaxed its control and when scarcity of fly in the area, associated with the long-term cycle, had encouraged such incursions ; once started, they proved impossible to stop completely, though they were kept within moderate bounds until the great drought of 1949 caused very wide-spread and long-lasting incursions. It is particularly noteworthy that of the three areas in which these invasions of cattle were greatest, two were in portions of the block where tsetse—*G. morsitans* in the one case, and *G. swynnertoni* with *G. pallidipes* in the second—had survived the longest. Though it was feared that the provision of such a source of food would have been of particular value to the persisting remnants of the fly communities, these fears proved groundless ; but it is still a puzzle as to why the large numbers of cattle available to the flies under these conditions did not prolong their survival sufficiently to allow some degree of recovery.

Discussion of Results.

In Nigeria, Lloyd, Johnson and Rawson (1927) excluded host animals from a fenced pond forming a dry-season secondary focus of *G. morsitans*, and at such times more or less isolated from other dry season foci. They observed a rise in the proportion of starving flies, a rise in the proportion of females and teneral flies in the catch, a rise in the proportion of avian blood taken, as well as of course a considerable fall in numbers. Against all these marked symptoms we can set (for *G. morsitans*) only a slight fall in the non-fatty dry weight, which may indicate malnutrition. For *G. swynnertoni* we are able to show a similar fall in dry weight and also a fall in fat, and a slight but real and progressive reduction in size of the flies themselves. We are unable to show any rise in the proportion of females and teneral flies, and the mean age of the flies did not materially alter. Finally we found no increase in the proportion of flies taking avian blood.

Compared with the Nigerian experiment our onslaught on the game was partial and slow, because as we were not working in a very small, fenced area, there was always a quantity of animals left ; and though the shooters were killing some of them we were not even trying to exterminate the small antelopes and pigs. It is evident that tsetse populations being slowly starved out over a period of several years may show only slight symptoms, which would hardly be of value in diagnosing states of nutrition in the field.

Cost and Practicability.

The experiment cost £50 per square mile, which is many times less than it would have cost to clear the area of bush, and doubtless much less than the cost of discriminative clearing of the tsetse habitats to the degree needed to destroy all three species of tsetse contained in it.

But the cost would have been enormously greater had the area not been isolated from the start ; it was already fly-proof on all four sides, and subject to considerable reinvasion by the game on the north side only, until the erection of the game fence there. The cost of isolation by fly-proof barrier clearings would have been too formidable for us to face, and had the work been carried out in order to eat into a solid fly-belt, the shooting would have had to penetrate to a depth at least 20 miles beyond the area which it was designed to free ; and since the habitat of the tsetses remains unchanged by shooting, this measure lacks finality in any area not isolated from the rest of the fly-infested bush. Either the shooting must continue indefinitely or an adequate fence must be erected and maintained, or else first the game and then the flies will slowly wander back.

Game destruction is thus inappropriate because indecisive except in isolated fly-belts of manageable size, and though discriminative bush clearing costs initially more it is greatly to be preferred wherever it is practicable and can assure success. By itself it does not provide a wholly permanent solution, but we have been much impressed by the slowness with which suitable habitats for *G. morsitans* and *G. swynnertoni* re-form, and at least some decades are likely to pass before the flies can return. Except therefore in fairly small, isolated areas, we should never recommend game destruction if discriminative clearing offered any hope.

We have not succeeded in finding whether the flies could support themselves on small antelopes and pigs, because we could not prevent shooters from destroying many of these as well as the larger species. It may very well be that the flies could survive on these small animals, seeing the length of time they took to die out as it was. The point has some practical importance, for it is probable that had the hunters paid for their own ammunition, as native hunters ordinarily do, they might have left these relatively unrewarding small animals alone, and this is always a possibility where uncontrolled shooting is allowed.

Summary.

Game animals were shot in an isolated area of some 600 sq. miles over a period of about five years. The density of animals was originally in the neighbourhood of 10 to the sq. mile.

This density is very low compared with densities recorded from national parks, and examination of the evidence available shows that the Tanganyikan bushland is understocked with game.

As the result of the shooting in the present experiment, two species of tsetse fly, *G. morsitans* and *G. swynnertoni*, were exterminated, and a third, *G. pallidipes*, was either exterminated or very heavily reduced. Experimental cattle then remained healthy in the area for 11 months, after which they were removed.

This result was achieved in spite of considerable invasion of the area by cattle, particularly intense at a late period when such an alternative source of food might have been expected to be particularly valuable to the tsetse.

There was evidence that the fat, residual dry weight and size of the flies decreased, but there was no apparent effect on mean age or the proportion of females in the catches, nor apparently did the flies turn to avian blood.

The cost was £50 per sq. mile ; but this figure would be very much greater in normal practice, with areas not isolated from the rest of the fly belt.

Game destruction is not recommended except in isolated areas of manageable size ; discriminative clearing of the habitats, even at initially greater cost, is preferable as offering a more lasting solution.

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THE ECOLOGY OF EPIDEMIC SLEEPING SICKNESS.
II.—THE EFFECTS OF AN EPIDEMIC.

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(Plate XIII.)

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Sleeping sickness has been one of the most serious killing diseases in tropical Africa, and it is natural to find that it has been responsible for considerable depopulation. In the West African epidemics, which have spread over such wide areas during the past 40 to 50 years, the strictly riverine habit of the vectors, *Glossina palpalis* (R.-D.) and *G. tachinoides* Westw., has been decisive in giving a characteristic pattern and complexity to the resulting depopulation. The river valleys were affected earlier and to a greater extent than elsewhere, and this had a disrupting effect on the distribution of the human population, with ecological, agricultural and domestic changes all contributing towards the impoverishment of the surviving sections of the population. In the course of these changes the rôle of the original depopulating agent often became obscured and difficult to trace. Moveover the relationship between the parasite, *Trypanosoma gambiense,* and its host, man, is, biologically speaking, fairly new ; a balance is not yet achieved, and the parasite tends to eliminate itself together with its host. By the time depopulation is so severe as to be obvious, the incidence of trypanosome infections has usually fallen through mortality of the human hosts and through the break in a close man-trypanosome-tsetse cycle due to the evacuation of heavily infected villages. It is only if an observer happens to be present at the peak of an epidemic that the true relation between trypanosomiasis and depopulation is obvious. Later, it may well be masked by secondary effects which have arisen through a changed environment.

In any attempt to explain depopulation two points must be borne in mind, the dynamic nature of the process, in which one change gives rise to another, and the fact that in tropical Africa man's greatest enemies lie in the forces of nature, which are better resisted by a higher population than a reduced one. Thus, as a population declines new strains are set up, and entirely new sets of factors may come into operation at different stages in the process. Observations made at any one stage may give a very misleading picture and the most careful reconstruction is necessary in order to decide what was the primary cause of the decline. If several lines of evidence can be used to cross-check one another the eventual reconstruction will be so much nearer the truth. The investigations described in this paper represent an application of these principles in tracing the effects of the severe sleeping sickness epidemic which struck the Upper Volta region of West Africa. Conclusions from this inquiry lead to discussions of the general relationship of *Glossina* to depopulation.

Depopulation.

Processes.

Sleeping sickness exerts a depopulating effect on a community in two distinct ways, through direct mortality attributable to the disease on the one hand and through a lowering of the rate of reproduction on the other. Among the few exact records of the effects due to direct mortality the most striking come from the Cameroons where the epidemic had reached extraordinary intensity in the early 1920's. For example, the Djem tribe were found, in 1926, to be 84 per cent. infected. In 1923 this tribe numbered 2,220 people ; by 1927 there remained only 642, of whom 540 were infected, mostly in an advanced state (Jamot, 1929). Infection rates in the Cameroons were exceptionally high, from 50 per cent. to 80 per cent. and whole tribes were threatened with extinction. The mortality that must have taken place in the more widespread epidemics of Nigeria and French West Africa can be judged from the indices of infection recorded when these outbreaks came to be surveyed. In Northern Nigeria the examination of 407,203 people during 1935 showed 20·5 per cent. to be infected with trypanosomiasis. Lester (1945) records a 12 per cent. decrease in the number of taxpayers in Zaria emirate as a result of the epidemic of 1923–33. In one district of the French Upper Volta Territory 11 per cent. of the population of 214,940 were found infected in 1940, and infection rates of over 15 per cent. were recorded in big sections of the neighbouring districts. Even at the lower infection rates, 5 to 10 per cent., which prevailed over a large part of the trans-Volta epidemic, it was common to find villages which showed, at a single survey, 20 to 50 per cent. of their inhabitants infected. The death rate among untreated cases is difficult to assess and it varies with different strains of trypanosome. For instance, a mild symptomless strain is present in the central belt of Nigeria, but McLetchie (1948) considers that most of these cases would die eventually from subsidiary causes induced by their low state of health rather than from the direct effect of the trypanosome. In most cases the mortality has been considerable, information, where available, showing that 20 to 70 per cent. of untreated cases die within a year. In areas of virulent infection 100 per cent. mortality was probably common.

Depopulation arises from trypanosomiasis indirectly through a lowering of the rate of reproduction, because of temporary sterility in infected persons of both sexes induced by endocrine disturbance (Muraz, unpublished report 1939 ; Saunders, unpublished report 1949), and because of increased infant mortality. The best study of both direct and indirect mortality was made by Harding (1940). Working in a heavily infected part of Zaria province in the middle of the extensive sleeping sickness belt of Northern Nigeria, he made estimates of death rate and infant mortality over a period of 15 months, and found that both of these factors showed a positive correlation with the incidence of trypanosomiasis. He estimated that the population, showing an infection rate of 20 per cent., had decreased at a rate of 20 per 1,000 in the 15 months. Since no cases of trypanosomiasis were seen among infants he concluded that the high infant mortality, which increased proportionally with the incidence of infection, was due to the inferior physique of babies born of infected mothers, or to inferior nursing, or to a combination of both. It was observed that an infant whose mother dies or ceases to give milk within the first few months usually perishes. To these factors could be added the general effect on a household, an effect impossible to measure but easily pictured. The rural household is living on a subsistence economy with little or no margin ; its maintenance requires and is dependent on the labour of all its members. The incapacitation of several people in a family, by a long and debilitating sickness, will lead to a falling off in the area cultivated, the upkeep of the buildings, the care of livestock and so on. A lowering of the standard of nutrition and general well-being in the family must be apparent long before mortality takes effect.

There is unanimity of opinion among those three widely experienced French authorities, Sicé, Muraz and Jamot, that trypanosomiasis, through its combined action of mortality, infant mortality and induced sterility, has been the most serious of the many depopulating factors operating in west and central Africa. They observe that in regions free from trypanosomiasis the population, naturally prolific, is almost always on the increase, whereas in infected regions the birth rate is invariably lower than the death rate, and that the gap between them becomes greater as the incidence of infection increases (Sicé, 1937 ; Muraz, *loc. cit.*). Since the sterility ceases if the patient is treated in time, and the health of the mothers, expectant and nursing, is also improved, it is to be expected that the widespread treatment of cases would effect a more rapid check on depopulation than could result from a mere decrease of mortality. In the central Nigerian sleeping sickness belt a considerable increase in population took place between 1933 and 1943, following the reduction of the disease by mass treatment (Lester, *loc. cit.*). The French mass treatment campaign was started in the heavily infected territory of the Upper Volta in 1939, and by 1946 they were already recording a reversal from a former serious population decline to a measurable increase. The speed of this recovery indicates the large part played by sterilisation and infant mortality in the total depopulating effect of sleeping sickness

Statistical studies.

When the combined surveys of trypanosomiasis and tsetse flies were started in the Gold Coast in 1937 close attention was paid to those areas where the epidemic was most severe. A very striking feature soon became apparent. The distribution of infection did not show a preponderance in places where the vector tsetse, *G. palpalis* and *G. tachinoides*, were most abundant, that is along the main rivers whose banks hold almost continuous fly-belt, but showed a tendency to concentrate along side streams and particularly their headwaters. A zone of unpopulated country, 4 to 10 miles wide, usually occurred along the larger fly-infested rivers, and within this zone ruined villages were found to be frequent. The ruins were in all stages, from a flattened mound dating back, it was estimated, to over 50 years, to quite recently abandoned compounds with standing walls (Pl.XIII, figs.5-6). There were occasional villages not completely deserted, one or two compounds out of perhaps 20 being still occupied, each by two, three or at most four individuals, predominantly old, with children conspicuously rare. These impoverished compounds (Pl. XIII, fig.3). showed up in striking contrast to the average Lobi family of a dozen or more with no lack of young folk. There was usually a profuse growth of grass and trees around the abandoned villages, and the older ruins were in process of being smothered by a dense regrowth of bush. In fact, the picture showed that severe depopulation of the riverside land had been taking place for at least 50 years and was still in progress.

These observations were made in two very different areas more than 100 miles apart : the Gambaga district in the north-east of the Gold Coast, drained by the White Volta and its tributaries, and the Lawra, Tumu and Wa districts in the north-west, drained by the Black Volta and the Kulpawn. The moderately populated Gambaga district is a country of sandstone hills with *G. palpalis* ubiquitous in the dense fringing forest along the swift streams. The epidemic was severe but probably comparatively recent, with completely ruined villages less conspicuous except along parts of the White Volta. The country in the north-west consists of metamorphosed granitic hills and wide, flat river plains, with *G. palpalis* and *G. tachinoides* common in the evergreen fringing forest which occurred, by no means uniformly, along the banks of the long meandering rivers. *G. morsitans* Westw. was present on both eastern and western sides of the country in the thinly populated parts where game abounded. In Lawra district, for the most part heavily populated, the epidemic was of long standing and ruins were conspicuous along the Black Volta and its two main tributaries, the Kamba and the Bakpong. Further south, in Wa district, the epidemic was locally severe and certainly of more recent origin (the southward shift of this epidemic has been described in the first part of this paper, (Morris, 1951)) and, very significantly, close to the Black Volta there are many villages which were, in 1940–1946, heavily infected with trypanosomiasis.

The people of Lawra district, who had sent over a thousand new cases of sleeping sickness to the hospital in 1938, were well aware of the adverse effect which the epidemic was having on their welfare. Elders in several villages were able to recount the history of the disease, and they were quite emphatic in attributing the majority of the ruins along the Volta and the Kamba to its ravages. They were able to recall that a sharp epidemic had hit the Lobi inhabitants of this area just before the beginning of the century, coming from the French side of the Volta where the sickness was more prevalent and had been present for a much longer time. Infection was brought across by natives who were sold into slavery on the British side after a series of bad harvests had reduced the French Lobis almost to starvation. Later, the slave raiders Samory and Babatu also caused a spread of infection away from the Volta. This early epidemic appears to have died down after some years, during which time it had spread over nearly half of Lawra district. However the sickness became noticeable again about 25 years ago, since when it has increased and spread until its recent severity.

Most of the ruins could be found marked as existing villages on an old map of Lawra dated 1907, and a map of Gambaga dated 1909 also showed villages close to the White Volta where there are only ruins today. Stories that sleeping sickness had been the depopulating factor were obtained from certain stretches of the White Volta but the evidence was less concise than that derived from Lawra. With the help of chiefs and elders of a section of this district along the Black Volta, where ruins were very noticeable and the sickness common in 1938, a survey was made of all ruined as well as occupied compounds, the age of each ruin being estimated both by observation and from the guide's information. The resulting map gave strong support to the natives' stories. It showed the complete evacuation of the settlements nearest to the Volta and its tsetse infested tributaries some 50 years ago, a later return to the well watered land of the riverside, and a renewed evacuation starting about 30 years ago and still in progress, with the majority of the population now living 3 or 4 miles, or more, from a main river.

In seeking confirmation of local history and of one's own interpretation of a situation that had already reached a fairly advanced state of depopulation, the first step was to see if there existed a relationship between the incidence of trypanosomiasis infection and the rate of change of population. Censuses in the Gold Coast had been taken in 1911, 1921 and 1931, but the earlier two were considered rather inaccurate and, as they had been made by districts only, were on too broad a scale for the purpose of this study. They did, however, provide suggestive evidence. For instance between 1921 and 1931 the Lawra-Tumu district, certainly the most heavily infected area at that time, showed the lowest rate of population increase for any district, only 10 per cent. compared with 35 per cent. for the Northern Territories as a whole, whereas the population of a district that was certainly free from human trypanosomiasis, Northern Mamprusi, had increased by 41 per cent. The 1931 census was more complete, citing population by villages, but on account of the war no census was taken in 1941. However, the mass treatment operations of the Trypanosomiasis Campaign under Dr. Saunders were organised on such careful lines, with every village visited by reliable enumerators, that data of village populations were at least as reliable as those from the 1931 census. This information provided both a check as to the population trend and an index of trypanosomiasis infection. For the latter figures to have their full significance they should come from an area unaffected by control measures. A survey made during 1939 of the then most heavily infected parts of Lawra, Tumu and Wa districts fulfilled this condition. The equally heavily infected Gambaga district was surveyed first in 1937, after a series of small anti-tsetse clearings had been made at every village in 1935–36. But since this measure had been carried out over the whole district and had resulted in a fall of only 15 per cent. in the incidence of infection by 1937, the mass of data available, 21,000 examinations in 1,200 square miles of country, was considered valuable enough for inclusion in the study. It has to be borne in mind that the Gambaga figures represent a slight underestimate of the incidence of infection which had actually been reached. This district was surveyed again in 1938–39, so the population figures from this second survey were comparable with those from the western side of the country, *i.e.*, they enabled calculation of the population trends in the two areas over an eight-year period from 1931. There were thus available for comparison figures of trypanosomiasis incidence and of population trends for a total population of 58,000 from two areas of active epidemic sleeping sickness. The number of examinations from the western area was 37,460 from 142 villages in approximately 1,500 square miles of country. For the sake of comparison, data from a lightly infected (0·1 per cent.) area just north of Gambaga district is included, as this shows the sort of population increase, 14 per cent., that took place in the absence of epidemic trypanosomiasis.

For examination of the two sets of figures for possible correlation the villages were grouped by areas in order to give samples of sufficient size, since many villages were small and some under 100 population. The areas chosen were homogeneous regarding

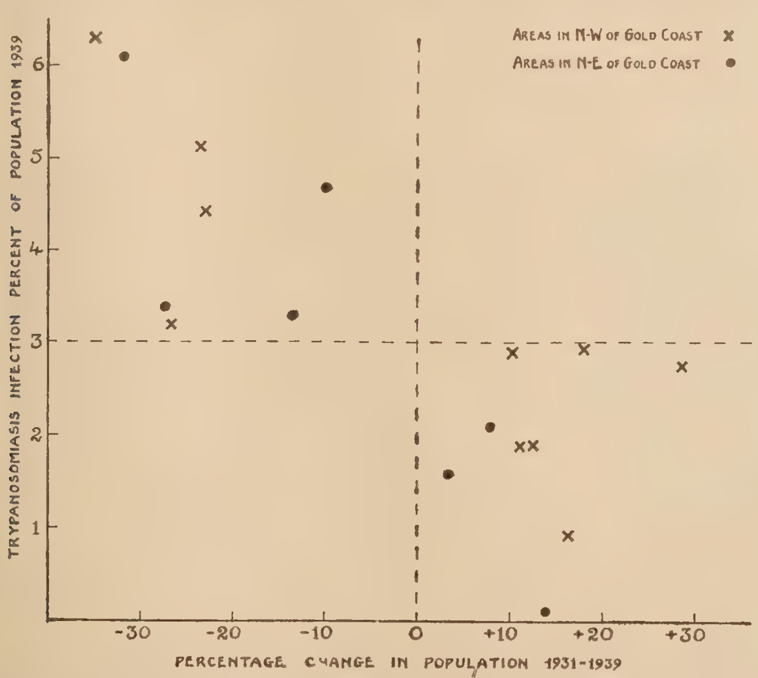


Fig. 1.—The depopulating effect of sleeping sickness. The correlation between population change and the incidence of infection in two areas of epidemic trypanosomiasis in the north of the Gold Coast. Each point represents an area of 100–250 square miles with 1,700–6,000 inhabitants.

natural features and human settlement, they varied from 100 to 250 square miles in extent, and represented the examination of 1,700 to 6,000 inhabitants. These groups were considered to be statistically valuable and representative of the prevailing rates of infection.

The results of this examination are shown graphically in fig. 1. It is evident that a close correlation exists between the degree of trypanosomiasis and the population trend, with a definitely depopulating effect coming into play at infection rates above 3 per cent. Below this figure the effect of trypanosomiasis may be operative or it may be overcome by factors favouring an increase in population. Increases of 18 per cent. and 29 per cent. in eight years, however, must be due to immigration as well as to natural increase and it is significant that the localities showing these population rises lie in the more recently infected area of Wa district and are located farthest from the heavily infected zone along the Black Volta. They may be showing that movement away from the focus of infection which had already been traced in Lawra.

It should be noted that data from the two widely separated areas with very different entomological and social conditions show similar trends. When allowance is made for the Gambaga figures being a slight under-estimate the closeness of the agreement will be seen.

These infection rates, taken from single surveys in both areas where there was a steady inflow of cases into treatment camps and hospitals, represent the minimum incidence affecting the population. The figures may be doubled to relate them to the " index de contamination " computed by the French Sleeping Sickness authorities, which more nearly represents the proportion of the population affected by the disease. Also they do not appear to conform with a statement by Saunders (unpublished, 1949) that " a population is stationary with a 6% rate ; it falls with a 13% rate ; and a 50% rate obliterates a village." This statement was based on infection rates for individual villages, which are always higher than the average rates for an area on which the present calculations were based.

The fact being established that serious depopulation was resulting from the present sleeping sickness epidemic, it was necessary to enquire whether the same effect would explain the extensive uninhabited areas along the Volta and its tributaries. The reason for suspecting trypanosomiasis as the primary cause lay in the proximity of the ruined villages to fly-belts of the vectors, *G. palpalis* and *G. tachinoides*. The plant associations forming the permanent habitat of these species represent the climax for the conditions prevailing on the rivers, pools and marshes where they occur. They are the most stable plant associations of the savanna woodland zone, they take a long time to develop, and those on the Volta and its major tributaries have probably been there for hundreds of years. Records of *G. palpalis* and *G. tachinoides* on the Black Volta go back to 1906 (Gouzien, unpublished, 1907), so it is safe to assume that the distribution of these tsetse on the main rivers has not altered materially at least during the past 50–60 years, the period with which we are concerned. The proximity to fly-belt thus affords a measurable factor which can be related to the older ruins. A correlation here would be valid if it can first be established that there is a relation between proximity to fly-belt and the incidence of trypanosomiasis.

Data for this study were obtained from large scale maps (1 : 50,000) which were made in the course of tsetse survey and control operations (Morris, 1946). The scale allowed distances from village to fly-belt to be measured as accurately as the variable conformation of the villages allowed. Uniformity was obtained by measuring to the nearest edge of the village. Measurements were usually confirmed on the ground. Information was taken from 43 villages to the east and south of Lawra, where the epidemic was active and had had no interference at the time (1939) of the trypanosomiasis survey. A decision had to be made as to what measurement should be used, since it was obvious that exposure of a village to *Glossina* was an extremely complex affair, depending not only on proximity but on such factors as the size and formation of the village (*e.g.*, a village of scattered compounds along the bank of a watercourse is far more exposed than a compact village in a similar place) or the amount of fly-belt close to the village (*e.g.*, the greatest contact between human beings and tsetse would occur within a bend or loop of a river or between two streams). It might also depend on the density of the tsetse within the fly-belt, but examination of data from 17 villages showed no correlation between incidence of sleeping sickness and fly density measured over a 2-year period (Morris, 1949). Various measurements were tried out ; for example the distance to the nearest heavily infested fly-belt was tried against distance to the nearest flybelt of any kind, however light, but the latter gave the closer correlation with the amount of infection. Again, the length of fly-belt within a mile radius of the village gave a poorer correlation than distance to the nearest point in the fly-belt. Given time it might have been possible to work out the complex relationships of exposure to tsetse, but with very urgent problems of control on hand this was out of the question. Moreover this straightforward measurement of the shortest distance between a village and the nearest permanent fly-belt of any kind is easy to make, whether in the field or from maps, and it does represent at its simplest the degree of danger to the villagers of coming into contact with tsetse in its own habitat and of the tsetse itself being carried into the village, which may be quite an important factor in an epidemic. This is the measure of proximity that was adopted. The data for the 43 villages is set out graphically in fig. 2.

This figure demonstrates clearly the existence of a marked relationship between the rate of sleeping sickness in a village and the proximity of that village to the nearest

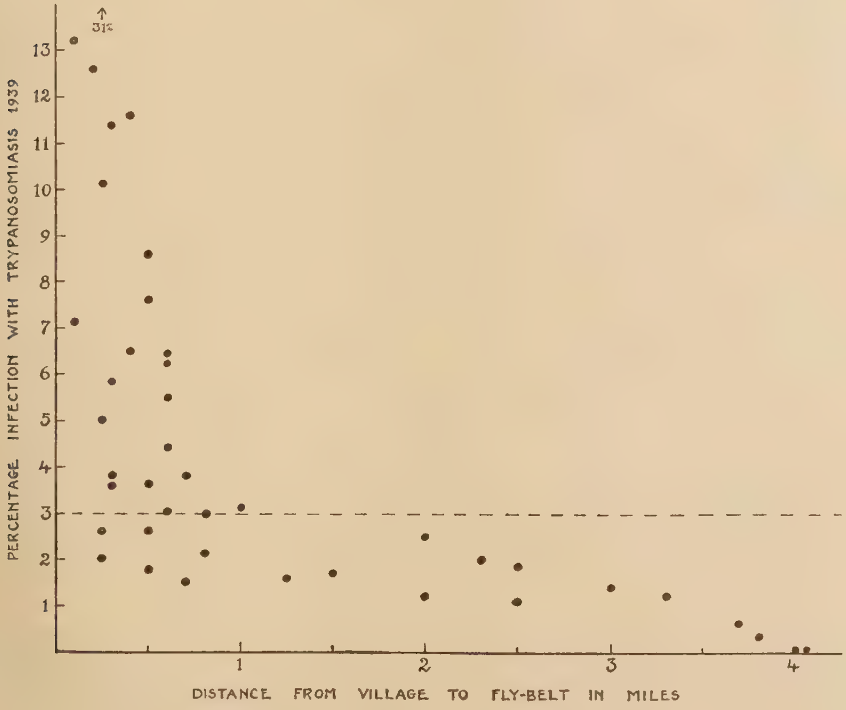


Fig. 2.—The relation between sleeping sickness incidence in villages and their proximity to permanent fly-belt of *Glossina palpalis* and *G. tachinoides*. From an active epidemic area in Lawra district, N.W. Gold Coast.

fly-belt of *G. palpalis* and *G. tachinoides*. Villages lying within one mile of fly-belt are exposed to the danger of serious trypanosomiasis infection, with very high infection rates occurring at closer proximity. Beyond a mile the danger is considerably less and at four miles infection need no longer be anticipated. This does not mean that it would not occur, as travellers can become infected miles from their home village. It is noteworthy that beyond the distance of a mile there is no occurrence of infections higher than the critical 3 per cent., the point, as has been shown, above which trypanosomiasis becomes a decisive factor in depopulation.

The next step was to examine the nature of any relation which might exist between the ruins and their proximity to fly-belt. Depopulation in individual villages was by no means always complete, so it was possible to get a measurable factor by counting the number of completely deserted compounds and expressing this as a percentage of the total number of compounds, occupied and deserted. This count was made for 70 villages in a block of country including the Black Volta and Kamba Rivers where the epidemic had first struck. Proximity to fly-belt was estimated in the same was as in the previous investigation. The results are shown graphically in fig. 3. The similarity between this diagram and that for trypanosomiasis (fig. 2) is striking. The particularly significant fact is the abrupt rise in the extent of depopulation that occurs among villages a mile or less from fly-belt, that is within the zone in which the critical 3 per cent. infection rate appears. Owing to the great variation in the size of individual villages the data, as shown in the diagram, cannot be directly analysed but grouping the villages according to their distance from fly-belt reveals the existence of a correlation between depopulation and proximity to tsetse. The numbers of compounds, ruined and occupied, were summed for groups of villages lying within 0–$\frac{1}{4}$, $\frac{1}{4}$–$\frac{1}{2}$, $\frac{1}{2}$–$\frac{3}{4}$, etc. miles from fly-belt, and the percentage of ruins was calculated for each group, giving the following table :—

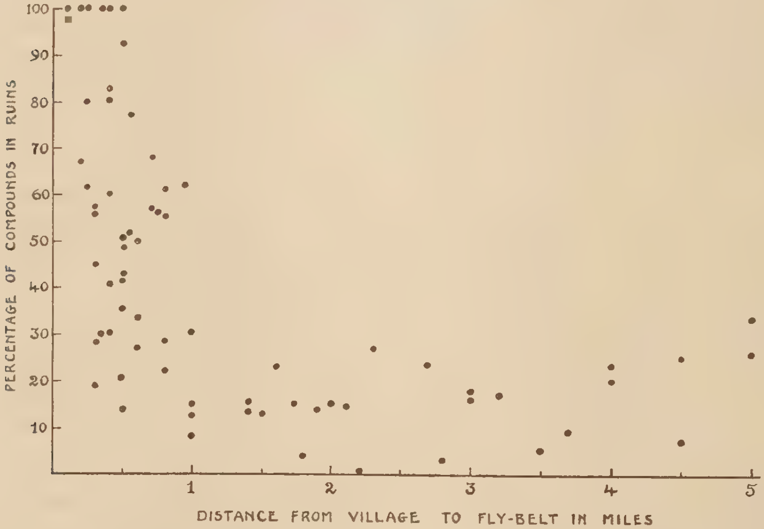


Fig. 3.—The relation between depopulation, measured by the percentage of ruined compounds per village, and proximity of the village to fly-belt (*Glossina palpalis* and *G. tachinoides*). From an area of long-standing epidemic trypanosomiasis in Lawra district, N.W. Gold Coast.

Distance from tsetse, in miles	0–·25	·25–·5	·5–·75	·75–1	1–1·5	1·5–2·5	2·5–3·5	3·5+
Percentage of compounds ruined ...	82	52	45	34	23	18	17	17

A much fuller interpretation of the data can now be given. It is evident that the far from permanent, mud built house goes into disuse, for one reason or another, to a quite appreciable degree, averaging 17 per cent. in those villages lying more than 2½ miles from the fly-belt. At such a distance it is clear, from figs. 1 and 2, that trypanosomiasis can have little direct effect as a depopulating agent. Rather more than this rate of delapidation becomes apparent in the group from 2½ to 1 miles from fly-belt, *i.e.*, where trypanosomiasis infection rates of about 2 per cent. appear, which, we have seen, may affect a population adversely. But it is within one mile that the abrupt jump in the proportion of ruins indicates that the disease has come into play as a decisive influence in depopulation, and at half a mile and less the proximity to tsetse can be critical, infection rates of such severity develop as to lead to the ultimate extinction of the village. Thus we find that the three sets of information build up the proof of sleeping sickness as a major, and a primary, depopulating factor in the areas of its epidemic spread.

Before accepting this result in its entirety it is important to enquire what other causes of depopulation might fit the distribution pattern under examination. An obvious suggestion is diseases that are water-borne or carried by insects associated with water. But the correlations have been made with the presence of *Glossina* and not just with the presence of water. In the area of this enquiry only ⅕–½ of the total lengths of river and tributary held permanent tsetse habitat, and although many of the fly-free streams are periodically dry there occurred, on granite formations where the sandy river banks were unsuited to support fly-belt vegetation, a number of stretches of permanent water free from tsetse. These were invariably centres of thriving settlements and showed marked population increases in contrast to the decreases found near to tsetse infested water. Malaria is seasonal and the Anopheline vectors show a very wide distribution in the wet season, and are more prevalent in the rice fields, borrow pits, ditches etc., which occur around any village, than along the main rivers with their strong flow. Schistosomiasis is most prevalent in the North Mamprusi district where a heavy population has been increasing for years. *Simulium* and its associated *Onchocerca* infection is common in only one or two localities on the Black Volta which are by no means coincident with the depopulated zones. Although this fly does become a pest seasonally on the thinly populated Kulpawn and Sissili rivers, and blindness from onchocerciasis is prevalent in many of the villages (B. B. Waddy, unpublished report), there is no evidence of these factors being the primary cause of the depopulation. Indeed in one of the most notorious localities for *Simulium* and onchocerciasis, the Funsi division of Wa District, a very definite increase in population took place between 1931 and 1948, not in one or two villages only but throughout the whole division. Smallpox, cerebrospinal meningitis and the 1919 influenza epidemic have all caused depopulation, but not particularly along the larger rivers. Slave raiding devastated many areas in the past but only just reached the Upper Black Volta, its worst effects having been felt farther south (the Ashantis,) farther east (Babatu) and farther west (Samory). Finally, there is soil exhaustion a great mover of populations. Had any of the river valleys been abandoned for this reason the cause would be obvious still. A Lobi farmer will not leave his land until it is practically reduced to sterility ; recovery from this state is very slow and the evidence is obvious for a long time. But no evidence of extensive soil exhaustion could be found by the writer or by agricultural officers who visited the depopulated areas, which are remarkable more for the abundance than for the poverty of their regenerating vegetation, an indication that the farms had been abandoned while still in a state of fertility. In contrast, severe exhaustion and erosion of the soil is strikingly apparent in much of the heavily populated country away from the tsetse infested rivers, an aspect of the problem which will be discussed later.

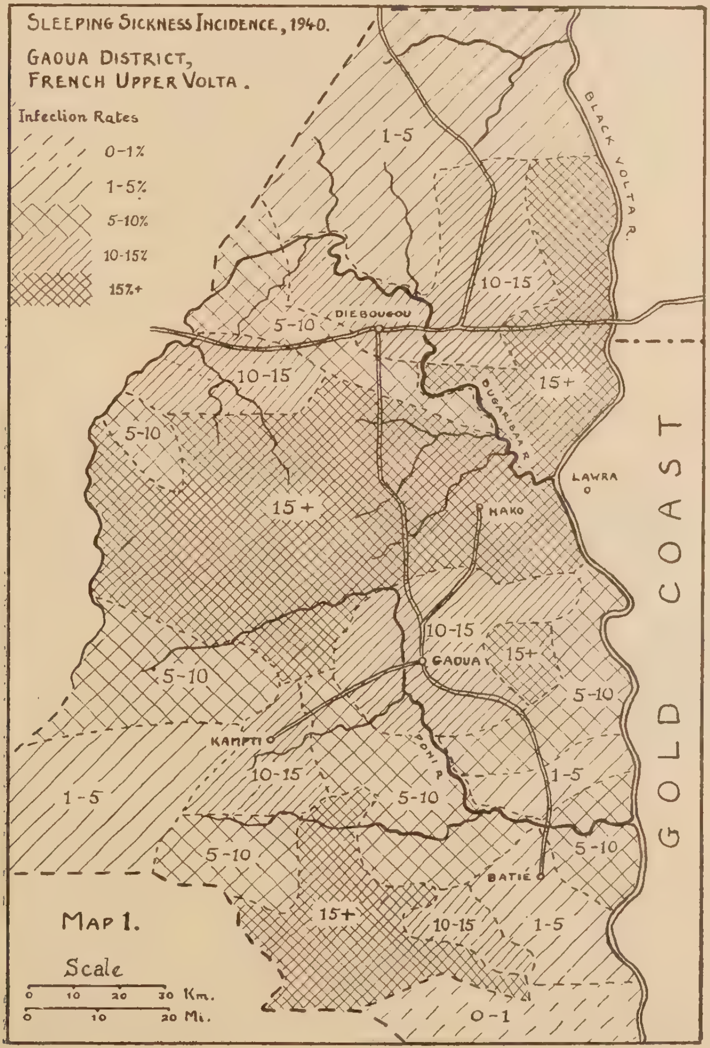
There was evidently no alternative explanation that would fit the facts of depopulation in the areas studied, but the most decisive evidence was forthcoming to confirm and complete the picture of sleeping sickness as a most destructive agent of depopulation here during the past 50 years.

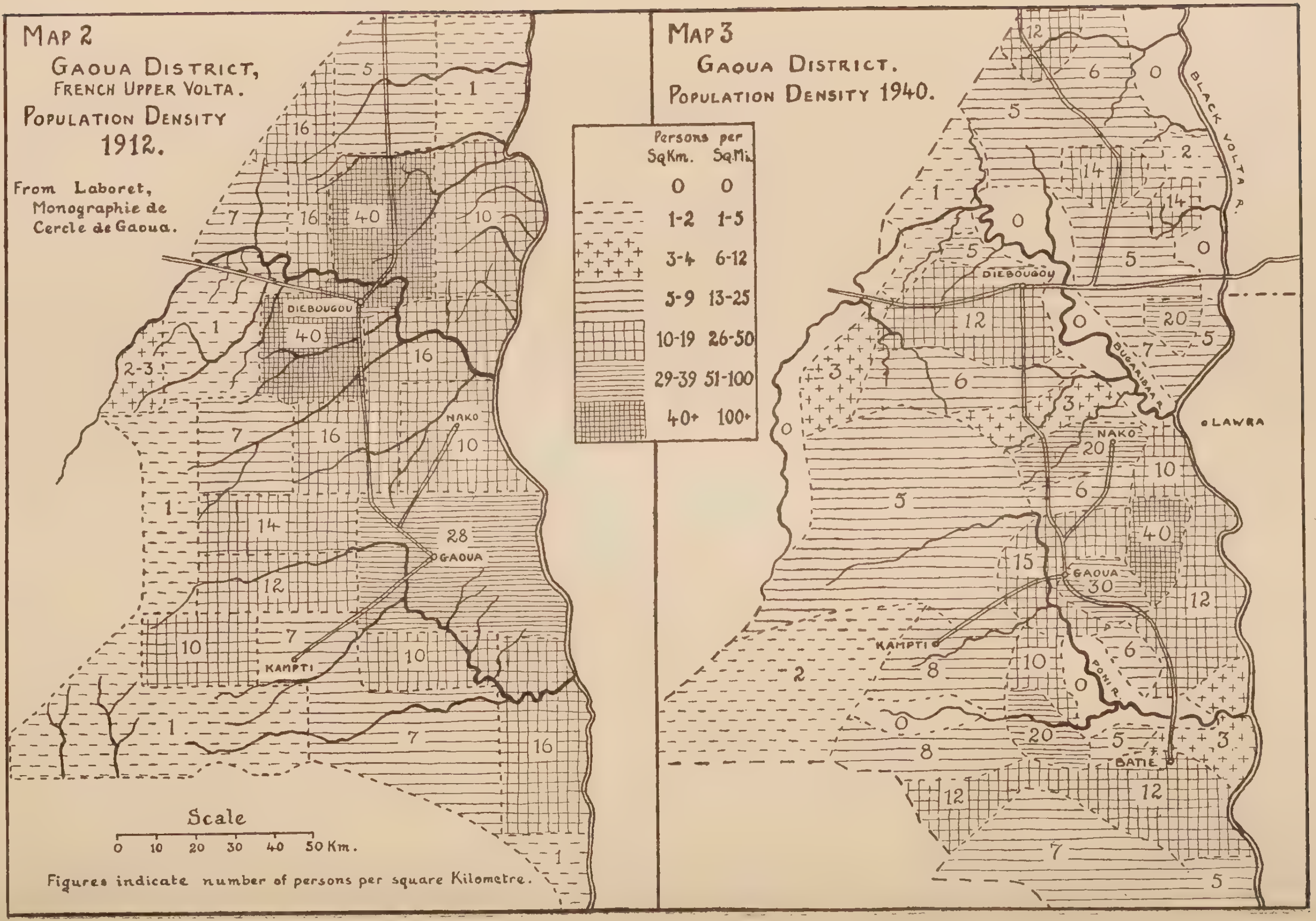
Information from records.

Subsequent to the completion of the statistical enquiry, records were obtained from French sources dating back to 1907, and including a detailed map of the population dated 1912. They refer to the country of the Black Volta west and north of the Lawra-Wa region, where the epidemic had been more widespread and severe. From them can be pieced together a much fuller picture than has so far been obtained of the ravages of the epidemic at a time when the lack of curative measures allowed it to proceed unchecked.

The information has already been quoted in the first part of this paper in the description of the development of the trans-Volta epidemic ; its severity and depopulating effects will now be discussed. Gouzien's report of 1907 (*l.c.*) gives ample evidence of the severity of the epidemic which was then prevailing along 100 miles of the Black Volta from Boromo to its northern bend. Here sleeping sickness had been present in serious form for certainly 25 years before Gouzien's visit, and probably much longer, and severe depopulation had already taken place among the communities that originally occupied the river banks. "All those who have recently traversed the region have noticed the desolation of the country between the Volta and the road from Boromo to Koury." Along most of the river not a single village was to be found on the actual banks although the river is easily navigable and full of fish. A few small settlements existed 1,500 to 2,000 metres from the banks, but it was only at 4 to 6 kilometres from the river that the bigger villages could be found. At that time (1905 and 1906) the epidemic was moving from the main river up the tributaries, and here severe manifestations were in evidence. Gouzien gives numerous examples, only two of which will be quoted here. Out of three villages on the same stream, Kaho, formerly flourishing with 800 to 1,000 inhabitants, was completely ruined ; Kosso had only 20 of its original inhabitants left ; and Nakosso had 400 victims since the sickness had first appeared 12 years previously. In the village of Bouna, with a population of 1,000, the disease was unknown until 1903, yet by 1906 a census showed that three-fifths of the population had disappeared and it was said that there had been scarcely a day without a death during the previous 18 months. Not a single child could be met here in 1907, and the chief said that in some weeks as many as five deaths occurred. Such was the speed with which sleeping sickness, unchecked, could strike a previously thriving community.

In the district of Gaoua, 150 miles farther south, the outbreaks though severe, were restricted at that time to localities on the Black Volta opposite Lawra and on its tributary the Poni River, west and south of Gaoua. Ruins were already conspicuous in these localities and the death rates in stricken villages were dangerously high. In villages that were investigated from 10 per cent. to nearly 20 per cent. of the inhabitants were known to have died in a year. Infection spread outward from these early foci until, by 1925, epidemics were appearing in many places and were soon decimating the populations of badly infected parts. During the next 15 years sleeping sickness brought a threat of depopulation to the entire district of Gaoua. Jamot's investigations, started here in 1932, revealed the alarming rates at which depopulation was proceeding (Muraz, *l. c.*). It was common for him to find villages which had lost from half to three-quarters of their population in the four years preceding his arrival, and the smaller hamlets were rapidly nearing extinction. In one canton, which had a population of 5,772 in 1929, Jamot could find only 3,821 in 1933, and of these, 505, or 13·2 per cent., were infected with trypanosomiasis. The inhabitants of a group of seven villages in a neighbouring canton had been literally decimated during the early stages of the outbreak and had regrouped at one centre, Yale, where there were 195 survivors in 1928. In 1932 there remained only 30 people, among whom 12 cases were diagnosed. Another small canton with a population of 1,500 in 1928 had lost 1,000 by 1932. Within six months of his arrival Jamot had discovered 3,329 cases of sleeping sickness, and out of 280 villages visited only eight were free from the disease. Infection rates in different villages varied from 2 per cent. to 52 per cent., and the averages for cantons ran from 9 per cent. to 17 per cent. At these rates the complete break up of the tribes of this district would have been certain. The catastrophy was averted only


SLEEPING SICKNESS INCIDENCE, 1940.
GAOUA DISTRICT,
FRENCH UPPER VOLTA.
Infection Rates
0-1%
1-5%
5-10%
10-15%
15%+
1-5
10-15
DIEBOUGOU
5-10
BLACK VOLTA R.
10-15
15+
BOUGOURIBA R.
5-10
LAWRA
15+
HAKO
GOLD COAST
10-15
GAOUA
15+
5-10
5-10
KAMPTI
PONI R.
10-15
5-10
1-5
1-5
5-10
5-10
BATIÉ
15+
10-15
1-5
0-1
MAP 1.
Scale
0 10 20 30 Km.
0 10 20 Mi.


Map 2
Gaoua District,
French Upper Volta.
Population Density
1912.
From Laboret,
Monographie de
Cercle de Gaoua.
Diebougou
Nako
Gaoua
Kampti
Scale
0 10 20 30 40 50 Km.
Figures indicate number of persons per square Kilometre.
Persons per
Sq.Km. Sq.Mi.
0 0
1-2 1-5
3-4 6-12
5-9 13-25
10-19 26-50
29-39 51-100
40+ 100+
Map 3
Gaoua District.
Population Density 1940.
Black Volta R.
Diebougou
Bugariba R.
Lawra
Nako
Gaoua
Poni R.
Kampti
Batie

by the well organised and widely applied system of mass treatment and anti-tsetse clearing which was started by the French Sleeping Sickness Service in 1939. Their surveys of the district of Gaoua, completed in 1940, showed the full gravity of the situation (Map 1). In a district with 214,950 inhabitants 25,426 cases of trypanosomiasis were found ; 11 per cent. of the population were infected.

It was impossible to estimate the loss of life in this and other parts affected by the huge epidemic which spread across the country of the Upper Volta rivers. There is a dearth of statistical data, so that a map showing the population of the Gaoua district in 1912 is especially valuable. This map comes from a monograph on the Lobi tribes of that area written by Laboret (" Monographie de Cercle de Gaoua," MSS. seen at Gaoua), and there is no reason to doubt the accuracy of the information gathered by this careful anthropologist. The original is on a scale of 1 : 1,000,000, and an exact copy is given in Map 2. In comparison with later, more accurate maps there are some unconformities regarding the rivers, and the introduction of motor traffic necessitated alterations to roads, but the general agreement is close.

At the time this map was made sleeping sickness was only beginning to spread away from its original narrow foci on the Volta and Poni Rivers, and its effect had not begun to be felt in the district as a whole. The Lobi are a naturally prolific tribe and were enjoying, for the most part, a rich soil from which they obtained ample crops. The population density averaged 30 per square mile for the whole district, but the people were settled mainly in the well-watered country neighbouring the Volta and its two major tributaries, the Poni and the Bugaribaa, and in the vicinity of the two principal towns Gaoua and Diebougou.

The effects of the epidemic can be seen from a comparison of the population in 1912 with that in 1940 as shown in Map 3. This map has been compiled from data very kindly supplied by the French Sleeping Sickness Service, and with first-hand acquaintance with the area. The break-up of the population so graphically described by Jamot and Muraz is only too apparent. It is especially evident in the subdivision of Diebougou where the epidemic had attained its greatest severity and the greatest fall in population had occurred. Depopulation is most conspicuous in the region of the Volta and along the Bugaribaa and its tributaries which were the natural avenues for the spread of infection into the heart of the district. The epidemic had progressed so far that even away from the big rivers there remained only two or three islands of moderately well-populated country. Farther south, from Nako to Batie, the epidemic was checked by the start of control measures before it had attained such widespread proportions, and depopulation was at the stage of emptying the country along the big rivers and concentrating the inhabitants on to the inter-riverine land. Taking the District as a whole the population density had fallen from 30 per square mile in 1912 to below 20 per square mile in 1940. With the population at the latter date standing at 215,000 it is safe to assume that over 100,000 people were lost since 1912. We do not know what the population might have been had this epidemic not occurred, but, judging by similar tribes in neighbouring country where infection was absent or sparse, there would certainly have been an increase, of the nature of 30 to 50 per cent., during the three decades. This is the measure against which to gauge the devastation wrought by sleeping sickness.

Displacement of Population.

Mention has already been made of the slow, outward spread of epidemic trypanosomiasis caused by the movement of people away from infected villages in an attempt to escape the disease. No cases have been met, or heard of, in which people consciously related the sickness to the presence of tsetse ; the water or fish may be blamed as poisonous, or infection held to be imported with corn or with cattle whereby the ground becomes infected. When histories could be traced it seemed usual for the whole village to have moved at once after the mortality had become serious, in some cases 50 per cent. to 70 per cent. of the inhabitants having already died. But a settlement's dependence on surface water, in this savanna country with its six-months dry season, directed the movement up the tributaries and side streams, and it ceased only when the people either had reached a source of fly-free water or had been driven to sites three or four miles back from the tsetse-infested stream, the distance beyond which the danger of infection becomes insignificant. In anything but a thinly populated district the movement will result in a concentration between the main rivers with their continuous belts of *G. palpalis* and *G. tachinoides*, and there arises the anomaly of overpopulation on headwaters and watersheds while the river valleys remain empty. This is a characteristic stage in an epidemic, when depopulation is local rather than widespread, and it is the result of mortality, lowered birth rate, and movement away from rivers. This stage is not stable ; the demands for water, farm land and grazing make a movement back to the river inevitable sooner or later, and so the epidemic is maintained until it reaches the state of widespread depopulation such as had occurred in the district of Diebougou. The stage of local depopulation, better described as displacement of population, is very important, being that in which a number of secondary factors begin to operate against the well-being of the people.

In 1938, when the present investigations were started, population displacement was widespread in the French Haute Volta territory and was shown typically in the Lawra district of the Gold Coast. A census made by the Lawra District Commissioner in 1942 made it possible for a population map of the area to be constructed (Map 4). The positions of completely ruined villages are marked in, also the distribution of the three species of *Glossina* present. The presence of *G. palpalis* and *G. tachinoides* commonly, though not invariably, indicates the presence of permanent water.

A study of the areas neighbouring the Lower Kamba and the Black Volta north of Lawra, where the epidemic had been longest in operation, shows well how the movement of population away from these rivers built up abnormally high population densities on the adjacent watersheds near Lawra and Nandom. The population distribution here is quite atypical for the district, with the steep gradients in densities, 200–100–0 per square mile, occurring in a traverse of 2 or 3 miles where the influence of the Volta and Kamba epidemics had been strong. On the two upper branches of the Kamba and on the Tizza River immediately to the south a more normal distribution is apparent, with the main population occupying the river valleys. In these parts the epidemic was more recent, and infection rates had, in 1939, reached very high figures in such places as Ulu, Tizza and Sabuli, where there were still good populations in close contact with the tsetse. The epidemic here was at its peak (see Map 1, Morris 1949, for distribution of infection), and the sequel would undoubtedly have been the displacement of population following the pattern of the lower Kamba. By this time, however, medical treatment and entomological control were established and had the effect, by reducing mortality and so reassuring the people, of checking the process of displacement.

The effects of displacement of population on the life of the community fall into two categories, those arising from a concentration of population on land away from the rivers, and those arising from the abandonment of the river valleys.

Concentration away from rivers.

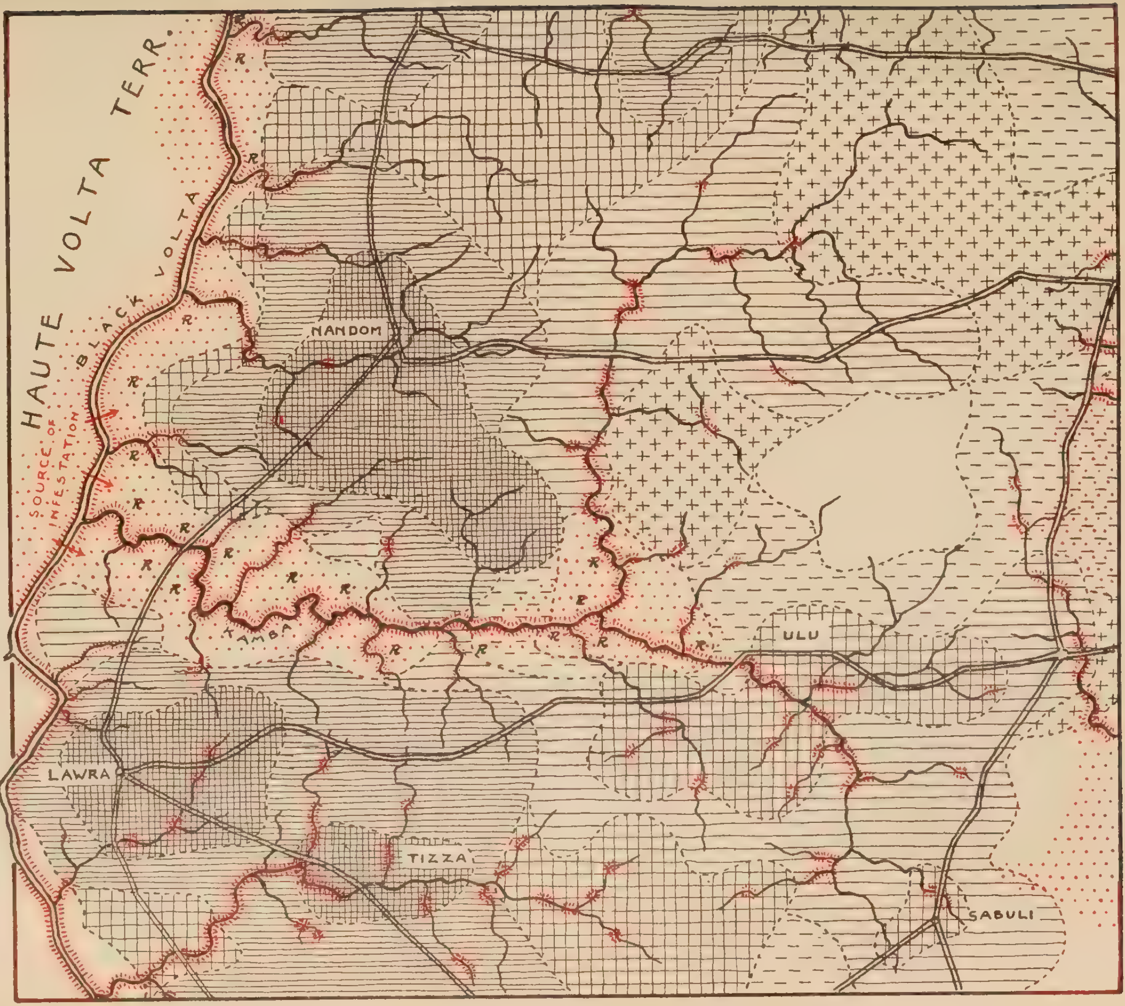
The cultivation of a river plain or valley differs greatly from cultivation on an upland. The change from one locality to the other, when people were forced away from the larger rivers, involved big changes in agricultural procedure and even in the kind and proportion of crops grown. The changes were rarely for the better. The higher water table in the valleys and the greater retention of the early rains, which are so valuable for the planting season, means that the season on the lower ground may be as much as six weeks ahead of that on closely adjacent uplands

MAP 4

RELATION OF POPULATION TO TSETSE, FOLLOWING EPIDEMIC SLEEPING SICKNESS.

LAWRA DISTRICT, GOLD COAST.

SHOWING DISPLACEMENT OF PEOPLE FROM KAMBA & VOLTA VALLEYS AND INVASION BY *Glossina morsitans*.


Permanent habitat of G. palpalis & G. tachinoides before control
Area occupied by G. morsitans Invasion of Kamba valley started 1939; maximum 1945; under control 1947.
Villages completely ruined R
POPULATION DENSITY, 1942. No: of persons per square mile
0
1 - 12
13 - 25
26 - 50
51-100
101-200
200+
Scale
0 2 4 6 8 Miles
HAUTE VOLTA TERR.
BLACK VOLTA
SOURCE OF INFESTATION
NANDOM
KAMBA
ULU
LAWRA
TIZZA
SABULI
R

(Pl. XIII, figs. 1-2). The swamp land available to the river valley communities is valuable for dry season gardens, and is made to produce early crops of maize and beans before it is flooded, and rice and yams after. For cattle, the river valleys are essential for their dry season grazing and water.

The domestic economy of households forced to settle away from permanent water is also adversely affected. People living on the watersheds near Lawra and Nandom had to go 3, 4, or even 5 miles for water in the dry season and the same distance for firewood throughout the year. This is a daily task which falls to the women, on whom it puts a severe strain as an addition to their household and family duties. The rural African household is still a self-supporting unit, reliant on wild products for a great many of its commodities, from building materials to fruit, cooking fats, herbs and medicines. All these are more readily procurable along the rivers than on the dry overcrowded uplands.

By far the most serious of the evils were those arising through soil impoverishment in the areas where overcrowding was acute. On headwaters and watersheds overcrowding is more rapidly fatal to the land than on the gentler gradients of river plains and valleys. The country becomes deforested through the cultivation of every bit of suitable land and through the demand for firewood and building poles. Overgrazing plays its part, and necessitates the cattle being sent down to the valley pastures, where there may be losses from trypanosomiasis and from predators, also where their manure is no longer available for dressing the hill farms. Shortage of farm land means a shortening of the fallow period, and both the lack and ignorance of manure deny to the farmer the substitute for bush fallow. Consequently soil exhaustion sets in, and, without corrective measures, develops into erosion. There seem grave risks of these processes starting at population densities above 100 per square mile, with the existing primitive methods of agriculture. At densities above 200 per square mile erosion is bound to occur, and in serious form. Considerable parts of the Lawra district had reached these densities. Sampling by the Agricultural Officer in 1943 showed that crop yields in the heavily populated (250 per square mile) area round Nandom, just north of the Kamba, averaged only 60 per cent. of yields from still inhabited parts of the river. He reported that many of the farms were on extensively sheet-eroded soil and that the land was nearing complete exhaustion. Gully erosion was prominent on the hillsides, and there were frequent stretches of bare laterite pan in places where the loss of topsoil had been complete. These denuded areas were more obvious on the French side of the Volta, where this stage of population displacement had evidently been passed through at an earlier date.

Abandonment of the river valleys.

When man abandons the river valleys he is quickly replaced by the indigenous fauna. This is not a haphazard effect ; it follows from the principle that the requirements of the primitive African agricultural community are fundamentally the same as those of many of the wild fauna, and man's existence is bound by the same ecological laws. His habitat, in other words, is decided by the presence throughout the year of easily available water and of a soil capable of supporting a good vegetation. Thus as soon as man moves out wild life begins to move in. It is not a gradual colonisation starting with the more primitive types, but a rapid replacement by those animals whose requirements are close to man's, the big game. For man's activities often leave a richer environment than exists under natural conditions. The process had been observed in a sufficient number of abandoned village sites on these northern rivers, in both French and British territory, for a quite general pattern in the replacement to be discernible.

The soil in the farms, abandoned while still in a state of fertility, produces a luxuriant growth of grass, herbs and bush, which provides most attractive grazing and browsing for all the ungulates. Around the ruins the soil is so enriched that they are rapidly overgrown by dense groves, particularly of *Anogeissus schimperi* and *Acacia* spp., which afford shelter for all species of game from duiker to elephants (Pl. XIII, fig. 5). Food is provided by those same trees which the native valued and therefore preserved and encouraged around his villages and farms : *Parkia oliverii*, *Ficus gnaphalocarpa* and *Butyrospermum parkii* (Shea Nut) for their fruits, *Acacia albida* for its foliage and pods which are relished by cattle and goats and also by the antelopes, and *Cordia myxa* for its fibre (Pl. XIII, fig. 6). The sticky fruits of the latter are especially sought after by elephants, as are the fruit and foliage of shea, fig and acacias. Consequently these ruins, which are invariably situated close to water, provide both shelter and food for game, and play an important part in attracting it into the abandoned river valleys. It frequently happens, in the process of depopulation, that a few surviving families in a village will be clustered in one section while the abandoned compounds are already overgrown with dense groves, (Pl. XIII, fig. 4) which provide regular shelter for duiker, bushbuck, guinea-fowl and francolin. These animals are constantly raiding the farms, and during the rains, when grass is long and foliage dense, the larger antelopes and elephants will visit the groves at night and present an even more serious threat to the villagers' crops. In the farms of one such semi-abandoned village, 15 duiker and oribi were shot recently in three successive nights, all emerging from the *Acacia* groves where they hid by day ; and a month previously a farmer had lost his whole planting of 300 seed yams from a field less than 400 yards from his home, through a single night's raid by elephants.

A population already weakened by the drain of sleeping sickness cannot stand such losses, and the final abandonment of the river valleys may be due as much to the depredations of wild life as to the original cause of the decline. With the last villages gone the game population becomes firmly installed in the valley, increases, and begins to raid the farms of neighbouring settled areas. The cultivation of remote bush farms in the valley becomes quite impossible, and even its utilisation for grazing is a matter of risk, since the increase in ungulates is accompanied by an increase in predators which take serious toll of domestic stock. The risk to livestock is amplified in the final stage of the replacement, which arises with the appearance of the game tsetse, *G. morsitans*.

G. morsitans is dependent on game animals for its food, and, although it can and does feed on man and cattle, regular contact with game is essential for the maintenance of its communities. Its habitat requirements are the closed associations of savanna forest and the open associations of " hard pan " (short-grassed areas with clumps of *Tamarindus indica*, *Diospyros mespiliformis*, *Zizyphus*, *Acacia* and *Combretum* spp.) all of which occur along the river valleys though by no means confined to the river banks. Groves of *Anogeissus* and *Acacia campylacantha* and *A. sieberiana* afford very suitable habitat. So the ruins, which are frequently overgrown with these species, again come into prominence ; they provide the combination of habitat and a regular host supply necessary for the establishment and survival of *G. morsitans*.

The replacement of human population by game and *G. morsitans* was observed in three separate localities in the north of the Gold Coast and it took place extensively in the neighbouring territory of the French Upper Volta. In the Kamba valley it was possible to keep the process of colonisation under close observation. The first survey was made in 1937, when depopulation was still in progress on side streams after having emptied the greater part of the main valley. Game was present in large numbers but there were definitely no *G. morsitans*. The most careful search was made for this species because of the obvious suitability of habitat and hosts, and because it was known to exist in the neighbouring Kulpawn valley to the east and across the Black Volta to the west. Towards the end of 1938 two specimens of *G. morsitans* were caught on the lower Kamba, only 5 miles from the

Volta. By the middle of 1939 the fly was breeding in small numbers on the lower Kamba, and by 1940 it had occupied all the empty and thinly populated parts of the valley and specimens were caught 40 miles upstream from the Volta. Counts of the game that year showed 200 roan antelope in 120 square miles of depopulated country, over 60 hartebeeste and about 30 waterbuck, besides numerous kob, reedbuck and bushbuck and very many warthog. Duiker and oribi were abundant. This is an abnormally high head of game for West Africa and it represented an artificial concentration through lack of ranging space owing to the high human population on either side of the valley. Undoubtedly this concentration of hosts brought about the remarkably rapid spread and increase in *G. morsitans*. Between 1940, when the fly rounds were organised, and 1945, when control began to take effect, the numbers of this species increased 14-fold and, because of its wide ranging powers, it was threatening the livestock of the surrounding settled areas. The game, especially roan, pig and duiker, had made farming in the valley impossible, and leopard and lion were taking heavy toll of stock. Some outlying compounds lost all their sheep and goats to leopard, and lion were taking 80 to 100 cattle in the year. Conditions were similar along the Black Volta from Lawra to the northern border and had progressed further on the French side where, in addition to other game, elephants were numerous in the deserted country along the bigger rivers and were causing very serious damage to the farms of neighbouring settlements On the upper Kulpawn River, bordering Lawra district to the east, an increase in game and intrusion of *G. morsitans* from fly-belts further south were found to be taking place in 1939, following severe depopulation through trypanosomiasis. In the Gambaga district *G. morsitans* was found to have trebled the area it occupied and to have increased greatly in numbers between 1930 and 1939, that is to say during the period of depopulation due to trypanosomiasis (page 379). The areas of spread were those where the fall in population had been most severe, *i.e.*, along the White Volta and the Nasia Rivers.

The combination of game and *G. morsitans* is a fatal one. The game is not only responsible for the destruction of crops and livestock but serves as a reservoir of the trypanosomes pathogenic to cattle. All the game animals of the savanna country, including elephant and lion, have been found harbouring *Trypanosoma vivax* or *T. congolense* or both, and in *G. morsitans* country infection rates with these species can be very high ; 80 per cent. infection rate was found in antelopes in the Kamba area in 1942 to 1944. In this part of West Africa even the local dwarf shorthorn cattle, with their partial tolerance to trypanosomiasis transmitted by *G. palpalis* and *G. tachinoides*, cannot survive in the presence of *G. morsitans*. It is rapidly fatal to take the larger zebu stock into fly-belts of this species. Although *G. morsitans* is the main vector of the *T. rhodesiense* form of human trypanosomiasis in East Africa its rôle in the case of the West African form of the disease caused by *T. gambiense* is more doubtful. In the laboratory it transmits this trypanosome readily, but transmission in the field depends on close and repeated contact between tsetse and man, conditions that are favoured by the restricted movement of the riverine tsetse in their confined habitat. The conditions favouring transmission are not often fulfilled in West Africa in the case of *G. morsitans*, with its wider range of hosts and habitat, but two instances have come to notice in the Gold Coast in which this species was undoubtedly involved in small outbreaks (Saunders, *loc. cit.*) and it must, therefore, be held under suspicion as an added danger to man in a situation already serious.

Thus the river valleys become inhospitable to man once the balance is tipped in favour of wild life. Agriculture and animal husbandry become equally impossible and have to be confined within the limits of the settlements, which may be favoured by the possession of tsetse-free water or may be those forced back three or four miles from the rivers. Overcrowding and over-use of the land arise in either case and the resultant erosion, in the absence of adequate manuring, is bound to bring about a reduction in the standards of living, of nutrition and of resistance to disease. The population will be subjected to an increasing complexity of strains in the changed and changing environment into which it has been forced. It seems doubtful if, without outside intervention, recovery would be possible.

The Wider Aspects of Depopulation.

The investigations which have been described were carried out in country where sleeping sickness was known to have been epidemic for a long time, records of severe outbreaks dating back to 1868. At the time when active interest was aroused by the epidemics, between 1930 and 1940, parts of the country were depopulated, either completely or partially. The different lines of evidence which it has been possible to trace all lead to the conclusion that sleeping sickness was the true depopulating factor, both historical and statistical evidence showing that the process of depopulation started only when the disease attained a certain severity and that it developed together with the rise in the epidemics. As depopulation proceeded other contributory factors entered into the process, seriously upsetting the domestic and agricultural life of the people to such an extent that, in the advanced stages, these secondary factors possibly weighed as heavily against the general welfare of the farming communities as did the primary factor of sleeping sickness.

A very interesting shift in importance from one species of tsetse to another can be seen to have taken place during the course of this depopulation. In the area studied the most severe epidemics were associated with the presence of *G. palpalis*, either alone or together with *G. tachinoides*, the particular attachment of the former species to human hosts rendering it the more potent vector in nature. Wide epidemics did occur in the presence of *G. tachinoides* alone, but they were less severe and they arose in the extreme north where this tsetse was forced, by limitations of habitat, to simulate the behaviour of *G. palpalis* in its association with human settlements (Morris, 1949). Severe epidemics were also dependent on a human population sufficiently high for their development, something well over 20 per square mile ; *i.e.*, they started in country unsuitable for *G. morsitans* because of the absence of game. This is the experience in the Gold Coast and, to judge from population maps, it holds good for the French territory also. The spread of the epidemic brought extensions into *G. morsitans* country, particularly along trade routes, but there was never the frequency of contact from village to village in such sparsely inhabited areas for widespread epidemics to develop. Only when depopulation emptied the river valleys did *G. morsitans* appear in the true epidemic areas, finally to dominate the locality with the disappearance of man. In these places *G. palpalis* is absent or sparse, probably because of lack of human food. For example on depopulated parts of the Kamba and Volta it was either absent or so rare as to suggest its being a migrant, whereas it was abundant on side streams and those parts of the main rivers where there was regular contact with people. Climate and vegetation were identical, there was only the absence of human hosts in the first case and its presence in the second to account for the difference in the fly's distribution. Thus we find, from the start to the peak of an epidemic, *G. palpalis* and perhaps *G. tachinoides* playing the dominant role, as the vectors of the human disease ; in the later stages *G. palpalis*, although present elsewhere and maintaining the spread of the disease, no longer prevails in the areas of the first outbreaks, *G. tachinoides* though present has lost its importance through the break in close contact with humans, and *G. morsitans* and its food hosts, the larger game, are exerting considerable pressure on the retreating population and are effectively blocking the re-occupation of the depopulated country.

The sequence of events which has been traced in the Upper Volta country is only one of several ways leading to the same end result, the domination of country, once well occupied by man, by *G. morsitans* and game. Depopulation from any cause can lead to the invasion of territory, which may previously have been fly-free, by tsetse of the *morsitans* group which then become a depopulating factor. Depopulation at this later stage is rarely due to mortality from human trypanosomiasis, but is caused by a retreat of the people on the loss of their stock, and, naturally, concerns tribes which are pastoral or which combine cattle raising with agriculture. The point at which the tsetse takes over the major rôle varies greatly, depending on the state of balance between man and his environment. It may require a series of disasters to upset a stable tribe to such an extent that the fly gets an entry. Ford (unpublished) has traced the sequence of catastrophies, rinderpest, smallpox, a plague of jiggers and finally administrative upsets, which broke up the agricultural and pastoral tribes of the Karagwe area of N.W. Tanganyika and finally led to the loss of the greater part of their country to *G. morsitans.* There is a huge sparsely populated central zone in the Northern Territories of the Gold Coast given over to game and *G. morsitans.* This country once held a good population ; the causes of its disappearance are multiple and difficult to trace, but a history has been obtained for one tribe, the Issalas of Tumu district. This tribe was badly cut up by Babatu's slave raiding before 1900 and, before it had fully recovered, it was decimated by the 1919 influenza pandemic. The village communities were then in such a state of numerical weakness that bad harvests, epidemics, etc., which would make little impression on stronger tribes, became disasters. Emigration sent the youths south to the big towns and mines. With loss of man power the practice of farming communally large tracts of bush fell off, and the abandonment of many farms and villages resulted in an increase in game and invasion by *G. morsitans.* Over perhaps half of the district these two agents are now the chief factors in depopulation. In outlying villages the whole of the livestock has been lost, shifting cultivation in bush farms is impossible because of raiding game, and the whole burden of production is thrown on fixed farms around the compounds. Yet without manure or a knowledge of fixed cultivation these inadequate patches cannot yield even a subsistence and the people, chronically underfed, are forced to supplement their harvests with wild fruits and herbs. They are too poor to possess firearms either for providing themselves with meat or for driving off raiding game which, in consequence, continues to increase. As in the case of Karagwe, the history of the decline goes back for over 50 years and involves a series of stages before the entry of the game tsetse as an important factor. In contrast are many of the instances recorded from East and Central Africa where game is more abundant and population thinner. The balance between man and fly is there so delicate that a quite minor upset to man's stability can bring about an increase in tsetse, which at once take on the rôle of depopulating agent. Swynnerton (1925) cites cases of an unpopular chief on the one hand, and the deposition of a popular one on the other, causing local depopulation, upgrowth of bush and influx of *G. morsitans* which then drove the main population out of their country.

These are cases, and many others could be quoted, in which *Glossina* is truly a secondary factor since its presence is due to a state of declining population initiated by some previous cause. But there are instances in which the initial depopulation can be attributed to an increase in tsetse, which is then the primary factor. There is the most interesting case studied by Jackson (1933) in the Central Province of Tanganyika, in which severe depopulation and loss of livestock was being caused by an advance of *G. morsitans* which seemed to be occurring spontaneously without any extrinsic contributary causes. It is sometimes possible to trace the process one step further back and explain the tsetse's increase. For example the cessation of the tribal custom of late grass burning in Uganda allowed the growth of thicket, the habitat of *G. morsitans* and *G. pallidipes,* both of which increased in different areas with devastating effects on the cattle-owning populations.

The correct analysis of these problems of depopulation and of their basic causes is of the greatest importance in devising and applying measures for their correction.

The defence against tsetse invasion exerted by a stable human population is a lesson that has long been appreciated (Swynnerton, 1923 ; Maclean, 1929), and it was soon realised that a settled population of sufficient size could be used as a means of attack against the game tsetse of the *morsitans* group. The sleeping sickness settlements of Maclean and Fairbairn in Tanganyika followed this principle (Fairbairn, 1948). The Sukumaland development scheme in the Mwanza Province of Tanganyika is a most promising enterprise on a large scale in which several thousand square miles of *G. morsitans* country have already been reclaimed by settlement on carefully planned lines, with no other measure against the fly. In all cases in which *Glossina* is a secondary factor in depopulation, settlement and development is the line of attack worthy of first consideration as likely to prove the most stable, and the most beneficial to the people concerned. This is the principle which is being followed in experiments to break up the large central *G. morsitans* belt in the Gold Coast.

Adherence to this principle should not blind us to the fact that in attaining the ideal solution it may be expeditious, or even necessary, to carry out some direct aggressive measures against the tsetse, particularly if it is associated with an abundance of game, itself a most disturbing factor, or when there is danger of human trypanosomiasis. When the tsetse has been the primary agent of depopulation direct measures against the fly itself will almost certainly be necessary in order to correct a situation that has become unbalanced. The key to the method of attack may be found in the history of events, for example the resumption of the practice of late grass burning is one of the methods being employed in campaigns that are proving successful against *G. pallidipes* and *G. morsitans* in Uganda. In the Gold Coast the problems, both direct and indirect, of human trypanosomiasis are being overcome by the eradication of the riverine tsetse, the process being taken even into the unpopulated parts of each river concerned in order to include the natural ecological systems. This makes it possible to correct the subsidiary effects arising from population displacement by bringing families down from the overcrowded uplands and settling them along the main river. In order to carry out this principle in the location of the original experiment on the Kamba River it was necessary to drive out the game, as much to protect the settlers as to get rid of *G. morsitans*. The control of this species, however, was far from complete as long as a large part of the lower river valley remained unpopulated, game and fly in small numbers continuing to intrude from the uncontrolled fly-belt across the Black Volta. It is only since the beginning of 1951 that the sufficient density of settlement of 15 persons per square mile has been obtained for it to be considered safe to relax hunting. The significant fact in this experiment is that since the change-over from hunting to settlement as a control method the intrusion of *G. morsitans* has practically ceased.

There is one final lesson to be learned from this study of depopulation. The control of sleeping sickness will remove one of the checks on population increase that have been operating in tropical Africa. Together with other improvements in health and the standard of living that are being brought about today this can be expected to accelerate the rate of increase in a naturally prolific people. This is one aspect of a world wide problem. Competent observers have estimated that, with current and expected trends, the population of Africa will be doubled within 50 years. It emphasises the vital necessity not only to correct existing problems, by the recovery of the land lost through sleeping sickness and other causes, but to ensure that this land is properly managed. The conquest of trypanosomiasis alone is not sufficient ; the solution of this one problem may raise others in its place. The plan for sleeping sickness control should be an integral part of a wider plan for tsetse control in which provision is made to ensure the full and proper use of reclaimed land by a stable and healthy agricultural community. Misuse of this land, especially practices leading to erosion or neglect, would mean literally failure to attain one's objective. The strength of such a plan will lie in the realisation that the requirements for good tsetse control are also the requirements for good husbandry.

Summary.

The most obvious effect of sleeping sickness is depopulation, which can be occasioned directly, through mortality from the disease, and indirectly, through a lowering of the reproductive rate of a community because of induced sterility and increased infant mortality.

The problem was studied in the north of the Gold Coast and the neighbouring French Upper Volta Territory, where severe epidemics have occurred, in localised form since at least the middle of last century, and in widespread form during the past 30 years. The vectors have been the riverine tsetse *Glossina palpalis* and *G. tachinoides*.

A close correlation was found to exist between the incidence of sleeping sickness and the population trend with a marked depopulating effect coming in at infection rates above 3 per cent. It was also found that both the rates of trypanosomiasis infection and the extent of depopulation showed closely similar relationships to the proximity of affected villages to the nearest flybelt.

These studies led to the conclusion that sleeping sickness had been directly responsible for the depopulation of large tracts of country along the Black Volta and its major tributaries. A proximity of one mile to fly-belt exposes a village to such severe infection that its chances of survival are endangered. It is only at 3–4 miles that the danger of infection ceases.

History obtained from French sources gives details of the severe losses due to sleeping sickness, dating from those occurring in individual towns and villages along the Black Volta at the beginning of the century to the widespread depopulation of whole districts by 1940.

The comparison of a population map of 1912 with one of 1940 shows the severity of the losses in one of the areas of the epidemic, it being estimated that over 100,000 people had been lost between those dates in a district with 214,950 inhabitants in 1940. Neighbouring districts free from the disease showed population increases of 30–50 per cent. in the same period.

In an advanced stage of the epidemic a characteristic pattern of population displacement appeared, with the main rivers completely or partially depopulated and a concentration of population taking place on headwaters and watersheds. This displacement was giving rise to profound ecological changes which brought an increasing pressure of adverse factors on the people. The movement to higher ground away from rivers necessitated changes in the agricultural and domestic life of a people accustomed to the easy proximity of water and grazing and the cultivations of a generally flat river plain. Acute overcrowding had resulted on some headwaters, and was leading to deforestation, soil exhaustion, erosion and their associated evils. The desertion of the river valleys was followed by the rapid regeneration of bush and invasion by wild life, especially the larger game animals, and later by the appearance of *G. morsitans*. At this stage, which had been reached in much of the territory of the epidemic, the loss of the river valleys for agriculture and grazing was complete and increasing numbers of game and *G. morsitans* were threatening the prosperity of adjacent agricultural communities.

The study of these events showed an interesting change-over in importance from one species of tsetse to another, depopulation having started with human trypanosomiasis carried by the riverine *G. palpalis* and *G. tachinoides* and ending with the domination of the country by *G. morsitans* and game. Depopulation from any cause is liable to be followed by the entry of the game tsetse which may then

become a dangerous factor in the process. It is possible to differentiate between *Glossina* as a primary cause of depopulation, when it has initiated the process, and as a secondary factor when it has entered at some later stage in a process already begun. The distinction has an important bearing on the question of control.

The most stable and generally satisfactory method of control of the game tsetse appears to lie in the establishment of a settled population of sufficient density and size, a measure that is sufficient in itself to eradicate the fly as long as it is a secondary factor in depopulation. It is considered that direct measures against the tsetse are necessary when it is a primary factor. Thus the situation in the north-west of the Gold Coast has been met by eradication of the riverine *G. palpalis* and *G. tachinoides* and resettlement of the depopulated parts of the river valley. The intrusion of *G. morsitans* ceased as soon as settlement to sufficient density was achieved.

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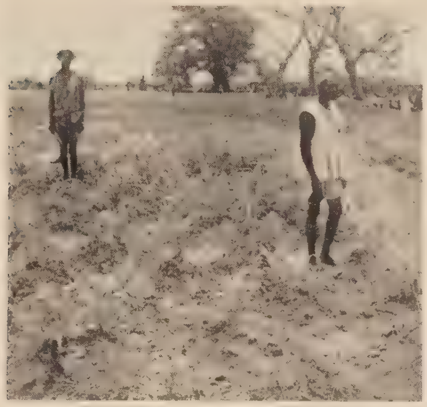

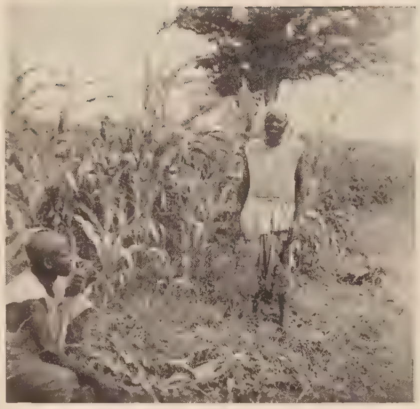

FIGS 1, 2. The diminishing productivity on an overcrowded upland owing to soil impoverishment and loss of early rain by run-off. The photographs, taken on 10th July, 1949, show the poor growth of maize on the over-populated (250 per sq. mile) watershed six miles north of the Kamba river (fig. 1), compared with a crop growing in the river valley (fig. 2).

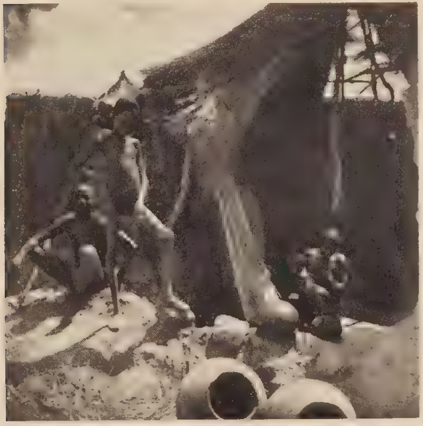

FIG. 3. The last stage before complete abandonment of a village. A reduced and impoverished family hang on in their derelict compound.

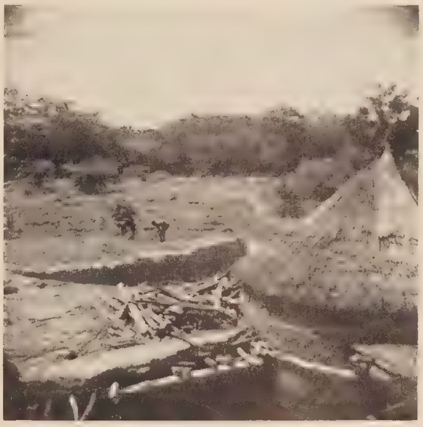

FIG. 4. The reduced man-power in the few remaining compounds of a once large village is incapable of keeping back the encroaching *Acacia campylacantha* woodland, in which game was becoming numerous.

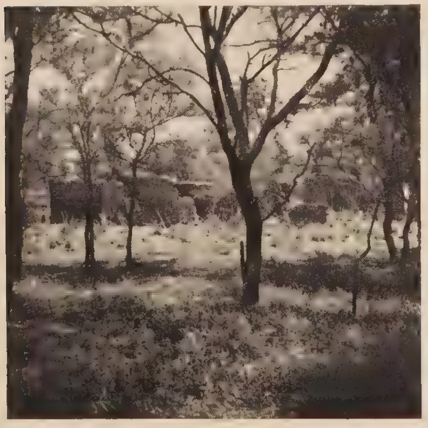

FIG. 5. Ruins, 10-15 years old, completely engulfed in *Acacia* woodland which formed a favoured habitat for game and *G. morsitans.*

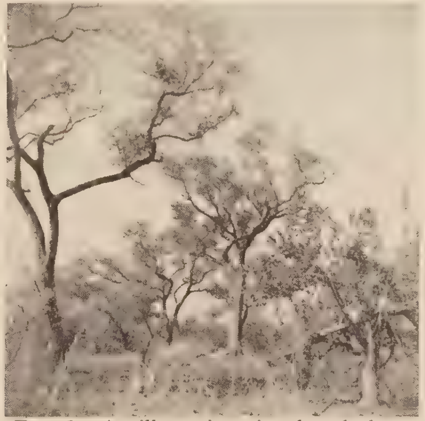

FIG. 6. A village site, abandoned about fifty years, with only flattened mounds remaining. Dominant *Acacia albida* (big trees) with *Cordia myxa* (bush in right hand corner with branches broken by elephant) and other species afford shelter and food for numerous game, which supported concentrations of *G. morsitans.*

ON A NEW PREDATORY MITE OF ECONOMIC IMPORTANCE.

By G. Owen Evans.

Dept. of Zoology, British Museum (Natural History).

E.M.I

The biology and systematics of the predatory mites of the family Laelaptidae have received increased attention since they have been shown to be of importance in the control of phytophagous mites, especially Tetranychidae, resistant to modern insecticides. The predatory mites of economic importance are almost entirely confined to the sub-family Phytoseiinae Berl., 1910.

Our present knowledge of the Phytoseiinae is based on the partial revision of the group by Nesbitt (1951). This work forms an excellent basis for future investigations on the group. In the present paper the terminology applicable to the chaetotaxy follows that of Garman (1948) which was adopted by Nesbitt (*loc. cit.*).

The species described in this paper as the type of a new genus was sent by Mr. E. R. Speyer, Cheshunt Research Station. The material was collected from tomato plants in the Canary Islands.

Phytoseiulus gen. n.

Body of both sexes covered by a single shield bearing 14 pairs of simple or slightly pectinated setae. Chaetotactic pattern characterised by the absence of D5 and M2, and by D4 and L4 being considerably longer than the other dorsal setae. In the female the sternal shield carries three pairs of simple setae and the ventri-anal *one* pair of preanals in addition to the paired paranals and the postanal seta. In the male the large ventri-anal shield bears three pairs of preanal setae and the movable digit of chela is provided with a distinct T-shaped process. The peritrematal plate extends around the posterior margin of the fourth coxa. The genual and basi-tarsal joints of Leg IV in both sexes are each provided with a long pectinated seta.

Type : *Phytoseiulus speyeri* sp. n.

In discussing the differences between the genus *Phytoseiulus* and the other genera included in the Phytoseiinae it will only be necessary to comment on the four genera *Typhlodromus* Scheuten 1857, *Amblyseius* Berl. 1915, *Kampimodromus* Nesbitt 1951 and *Phytoseius* Ribaga 1904, *i.e.*, those genera in which the number of setae on the dorsal shield does not exceed 18.

Phytoseiulus may be separated from *Typhlodromus*, *Amblyseius* and *Kampimodromus* by the absence of setae D5 and M2 in the chaetotactic pattern of the dorsum. In the presence of a few very long setae on the dorsal shield it bears some resemblance to *Amblyseius** but in the latter it is always L4, M2 and L9 which are considerably longer than the other dorsal setae. The new genus is most closely related to *Phytoseius* in that they both lack D2 and M2. *Phytoseius* differs, however, in having the dorsal shield strongly ornamented, in setae of the series D, with the exception of the verticals, being very short and simple and in the remainder of the setae of the dorsal shield being characteristically thickened and " thorny ".

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*Garman (1948) erected the sub-genus *Amblyseiopsis* for a species, *A. americanus*, in which the ventri-anal shield is narrower than the genital. Garman compared his species with *Amblyseius grandis* Berl. 1915 in which the ventri-anal shield is markedly wider than the genital. In the type species of the genus, *A. obtusus* (Koch) Berl., the width of the ventri-anal shield is intermediate between that of *grandis* and *americanus*. In view of this I do not consider the characters noted by Garman necessitate the erection of the sub-genus *Amblyseiopsis*.

The extreme length of setae D4 and the presence of only one pair of preanal setae in *Phytoseiulus speyeri* sp. n. is unique among the Phytoseiinae.

Phytoseiulus speyeri sp. n.

The form of the body varies according to the amount of pressure the specimen has suffered. The well-chitinised dorsal shield is oval, narrower in the anterior half and slightly truncated posteriorly. The colour in preserved specimens is reddish.

FEMALE.

The *dorsal shield* bears 14 pairs of setae comprising eight in a lateral series (L), five in a dorsal series (D) and one median (M)—fig. 1. Setae L1, 48–50 μ long, are situated a fair distance from the lateral margin of the shield and extend beyond the bases of the short setae L2. Setae L3 are approximately one-third the length of L4 (170 μ long) and lie internal to the line connecting L2 and L4. The setae L5, L6 and L7 are long; L5 measuring about 67 μ and slightly shorter than L6 and L7 which are equal in length. L7 is about one-third the length of L8 and lies external to the line connecting L6 and L8.

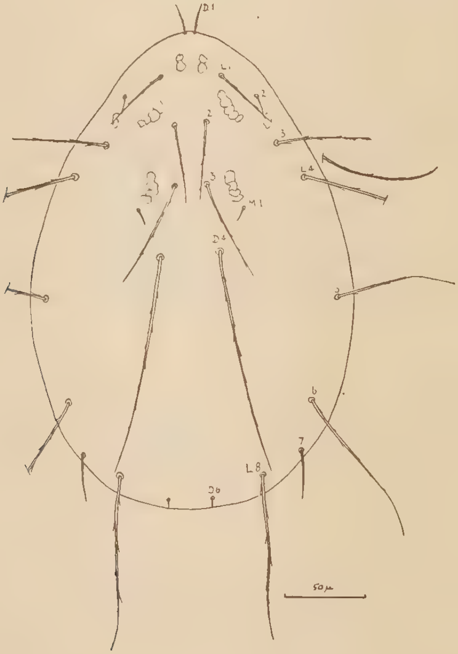

Fig. 1.—*Phytoseiulus speyeri* gen. et sp. n. ♀. Dorsal shield.

The dorsal series lacks D5. The vertical setae (D1) are one-half the length of D2 which measure 50–53 μ. Setae D3 (69–73 μ) are considerably shorter than D4 which extend almost to bases of L8. M1 equal to L2 and form a hexagon with setae D3 and D4. The paired setae D6 are the shortest of the dorsal setae and are situated between L8 on the posterior margin of the shield.

The dorsal setae are pectinated except L1, M1 and L7. The longer the setae the stronger appear to be the pectinations.

The scapular and lumbar setae are situated on the interscutal membrane.

The *ventral surface* is covered by the sternal, metasternal, genital and ventri-anal shields. The sternal shield shown in fig. 2A has three pairs of setae and two pairs of "pores". The sternal setae are approximately 60 μ long and smooth. The third pair are situated on postero-lateral projections of the shield. The metasternalia are small and the setae shorter than the sternals. The posterior margin of the genital shield is truncated and bears one pair of long setae. The ventri-anal shield is of the form shown in fig. 2B. It measures 92–95 μ long and 76–80 μ in its greatest breadth. In addition to the setae normally associated with the anal region there are a pair of pre-anals. The ornamentation of the ventri-anal shield is peculiar being composed of concentric rings of scale-like markings.

The peritremata reach almost to the level of setae L2. The form of the peritrematal plate is shown in fig. 2C.

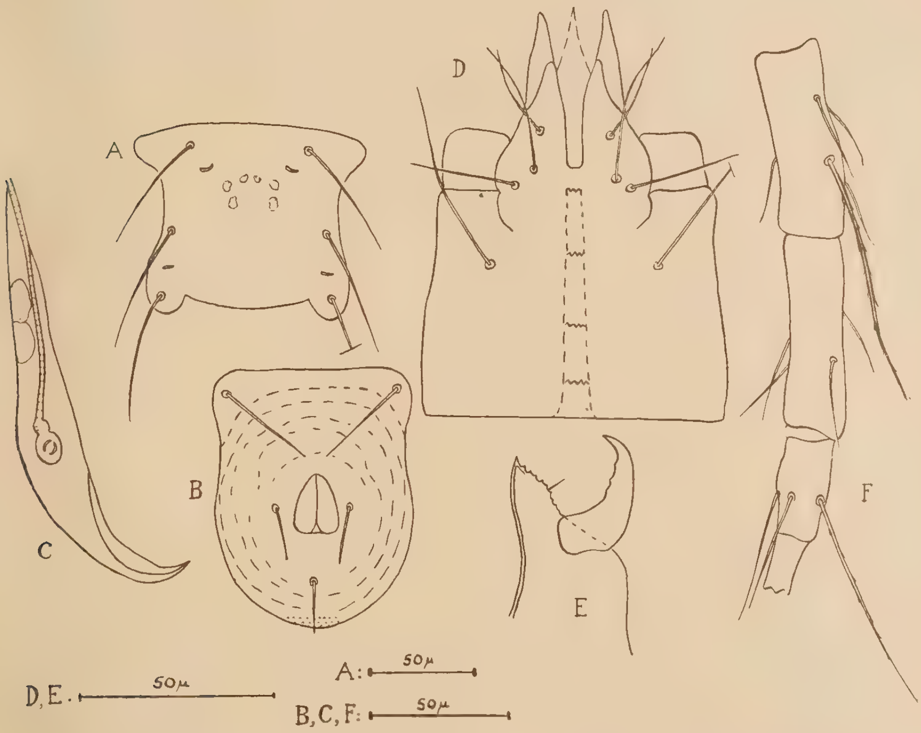

Fig. 2.—*Phytoseiulus speyeri* gen. et sp. n. ♀. A. Sternal shield. B. Ventri-anal shield. C. Peritrematal shield. D. Gnathosoma (Ventral). E. Chela. F. Genual, tibial and basi-tarsal joints of Leg IV.

The interscutal membrane bears, on either side of the ventri-anal shield, three setae antero-laterally and one seta postero-laterally. The latter is equal in length to L7 on the dorsal shield.

The *gnathosoma* carries four pairs of ventral setae (fig. 2D). The posterior pair are longer and stouter than the three pairs situated anteriorly. The maxillary palps are five segmented. The palp-femur has a spatulate seta internally and the forked seta on the palptarsus is two-pronged.

The chelicerae comprise a fixed and a movable digit. The former has about eight small teeth and a *pilus dentilis*. The movable digit is approximately 22 μ long and armed with four teeth of equal size on its cutting edge.

I was unable to see the form of the epistome in the material at my disposal.

Legs I to IV measure respectively 440, 340, 360 and 530 μ. The genual and basi-tarsal joints of Leg IV are each provided with a long pectinated seta (fig. 2F). The genu is 71 μ long and the associated seta 75 μ. The basi-tarsal joint, on the other hand, is 37 μ long and the pectinated seta 79 μ.

MALE.

The chaetotactic pattern on the dorsal shield is the same as in the female. The structures which require description are the ventri-anal shield, the chelicerae and the chaetotaxy of the fourth pair of legs.

The ventri-anal shield, length 115 μ, is shown in fig. 3A. Antero-laterally the shield is produced into a conspicuous horn ; this is seen clearly when the shield is compressed. The preanal setae, 25 μ long, are approximately equidistant from each other, *i.e.* the bases of the three setae on either of the shield form an equilateral triangle. The paranals and the postanal seta are relatively shorter in length. The form of the ornamentation is shown in fig. 3A.

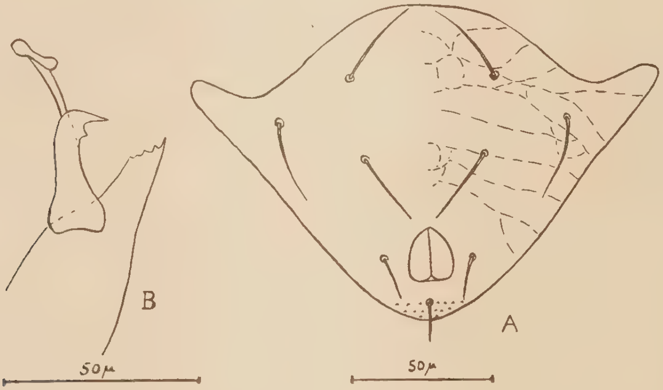

Fig. 3.—*Phytoseiulus speyeri* gen. et sp. n. ♂. A. Ventri-anal shield. B. Chela.

The chelicerae (fig. 3B) have the fixed and movable digit of equal length. The latter, length 15–16 μ, with a single tooth distally and a strong T-shaped process extending beyond the end of the digit. The fixed digit is almost parallel sided and " cut off " at an angle of about 45° distally. The dentition comprises four small teeth along the truncated edge.

Legs I to IV measure, respectively, 319, 251, 253 and 418 μ. The genual joint of Leg IV is two-thirds the length of the pectinated seta (62 μ) and the basi-tarsal seta three times the length of the basi-tarsal joint (27 μ).

DIMENSIONS.

The type material consists of two females and a single male. The measurements refer to the well-chitinised dorsal shield. Female—Length 300–305 μ, breadth 210–220 μ ; Male—Length 264 μ, breadth 158 μ.

LOCALITY.

The three specimens referred to above were collected with *Typhlodromus cucumeris* Oudms. from tomato plants in the Canary Islands. Both species were preying on *Tetranychus* sp.

The male and female types are deposited in the collections of the British Museum (Natural History).

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ON THE CONTROL BY INSECTICIDES OF *HETERONYCHUS CONSIMILIS* KOLBE (DYNASTIDAE), A SERIOUS PEST OF WHEAT IN KENYA.

By R. H. Le Pelley and W. H. Goddard.

The Dynastid beetle, *Heteronychus consimilis* Kolbe, is a major pest of wheat in the important wheat-growing areas of Ol Kalou and Ol Joro Orok (altitude 6,000–9,000 ft.) in Kenya. The adult normally lives in wheat lands or moves into wheat lands from grassland breeding-areas outside and is responsible for a large part of the damage ; it chews the young shoots just below the ground, and this may completely kill the plant. Whole fields may be destroyed, the wheat withering away completely. In several cases, three successive wheat plantings have been totally destroyed. On the other hand, the plants may not all be killed, and in such cases the beetles lay their eggs among the roots and the larvae do great damage by feeding on the roots up to the time when the wheat is almost mature.

Some early experiments in 1950 with BHC (benzene hexachloride) indicated that soil dressings might give control, and in 1951 it was decided to lay down a series of trials of various soil treatments. One of us (R. Le P.) was responsible for the general planning of the work, and the other (W. H. G.) for the running of the experiments, including all the field work involved. The field work included a study of the biology of the species concerned, but this was not completed and is not reported here. The results of the insecticide trials were striking and showed promise of practical control of the beetle, and the present paper has been written to make them available as soon as possible. In the experiments, the control of the adult beetles almost eliminated the later damage by the larvae. The work also holds promise of extension for the control of other soil-inhabiting insects, and experiments to this end are contemplated.

Experiments.

Experiment No. 1.

This was conducted on 28 strips, each of approximately one-tenth of an acre, 24 feet wide (*i.e.*, two drill widths) by 60 yards long. These strips were parallel to one another and alternated with untreated strips 12 feet wide to prevent appreciable movement of insects between one treated plot and another. Seven treatments, including the control, were applied, and were replicated four times in randomised blocks. The plots were planted with wheat on 22nd June 1951. Double superphosphate was applied as fertiliser at the rate of 90 lb. per acre on all of them except those that received treatment (4), on which it was greatly reduced for the reasons given below. The treatments were as follows :—

(1) Aldrin at the rate of 18 lb. of a 2½ per cent. dust per acre (7·2 oz. technical aldrin per acre), applied at the time of planting through the fertiliser attachment of the seed drill with double superphosphate mixed at the time of application. Plots treated were 3, 12, 21 and 27.

(2) BHC in the form of Mergamma A seed dressing (stated to contain 20 per cent. gamma BHC) at the rate of 10 oz. to a 200-lb. bag of seed wheat ; the seeding rate was 65 lb. per acre, resulting in the application of 3¼ oz. Mergamma A per acre. Plots treated were 2, 8, 18 and 25.

(3) BHC in the form of Agrocide 7 (stated to contain 2·6 per cent. gamma BHC) applied as a seed dressing at the rate of 10 lb. to a 200 lb. bag of seed wheat, or 3¼ lb. of Agrocide 7 per acre. Plots treated were 7, 11, 16 and 23.

(4) BHC in the form of Agrocide 3 (stated to contain 0·65 per cent. gamma BHC) at the rate of 8 lb. 5 oz. per acre applied at the time of planting through the fertiliser

attachment of the seed drill with double superphosphate mixed on the day of application. (As the mixture of double superphosphate and Agrocide 3 tended to block the drill, only 16 lb. 10 oz. double superphosphate was applied per acre ; this may have influenced the yield and this possibility should be borne in mind in interpreting the yield figures given later.) Plots treated were 1, 13, 17 and 28.

(5) BHC in the form of Agrocide 3 applied 24 days after planting, when the wheat was about 4 ins. high, with a rotary blower to the surface of the ground at the rate of 1 cwt. per acre. Plots treated were 6, 14, 20 and 24.

(6) BHC in the form of Agrocide wettable powder (stated to contain 6·5 per cent. gamma BHC) applied as a bran bait at the rate of 10 oz. wettable powder and 50 lb. bran per acre 24 days after planting. Plots treated were 5, 10, 15 and 26.

(7) Untreated control. Superphosphate fertiliser was applied. Plots treated were 4, 9, 19 and 22.

Experiment No. 2.

This experiment was conducted on a farm several miles away from that of No. 1. It was planned exactly as No. 1, except that in treatment (1) the rate of technical Aldrin was halved to 3·6 oz. per acre, but treatments (5) and (6) were not applied.

Experiment No. 3.

This experiment was conducted on a farm near that of No. 1. Treatments were as for No. 2. Beetles failed to appear in appreciable numbers in this experiment and it will therefore not be mentioned further.

Results.

Experiment No. 1.

From the commencement of the experiment, beetles were killed, many being found dead on the surface of the ground in some of the treatments. The first count was made on the fourth day after treatment and gave the following totals of dead beetles on the four plots of each treatment.

Treatment 1—830
2—510
3—252
4—111
7— 3

(Treatments 5 and 6 had not been applied at this time.)

The dead beetles were removed and counts were made every few days. Killing continued up to 47 days after planting ; the counts were then discontinued. The totals of dead beetles are given in the following table, in which plot 1 is the plot with the lowest reference number of the four for any particular treatment, plot 2 is the one with the next number in the same treatment, and so on. It will be seen that the population of beetles increased markedly towards that end of the series of strips with the higher numbers.

The distribution of the insects in the conditions of this experiment were considered to depart so far from normality that the figures were transformed by using the function, log. $(1+x)$. This gave transformed variates for totals as shown in the last line of the table. The least significant difference at $p=0{\cdot}05$ is 1·14. All treatments, therefore, except No. (6) (BHC bran bait) were significantly better than the control. Aldrin had a greater total kill than any other treatment, but was not quite significantly better than Mergamma A or Agrocide 7, which were not significantly

Plots	Aldrin	Mergamma A	Agrocide 7	Agrocide 3 with fertiliser	Agrocide 3 applied with blower	Agrocide bait	Untreated
	1	2	3	4	5	6	7
1	169	116	284	52	24	16	6
2	735	548	549	371	49	18	17
3	777	795	353	262	37	23	26
4	2,417	1,543	981	913	36	63	35
Totals ...	4,098	3,002	2,167	1,598	146	120	84
Transformed variates, log. (1+x)	11·37	10·90	10·74	9·68	6·24	5·70	5·09

different from one another. Mergamma A was significantly better than Agrocide 3 applied with the fertiliser, but Agrocide 7 was not quite significantly better than Agrocide 3. All these were significantly better than Agrocide 3 applied with a rotary blower, which was not significantly better than Agrocide wettable bran bait. The plots were separately harvested in January 1952, after a very wet season which resulted in the crop being weather-beaten. Nevertheless, most of it was satisfactorily harvested by combine, so that reasonably accurate data were obtained. The following table gives the yield of wheat in pounds per plot.

Plots	Aldrin	Mergamma A	Agrocide 7	Agrocide 3 with fertiliser	Agrocide 3 applied with blower	Agrocide bait	Untreated
	1	2	3	4	5	6	7
1	125	103	114	92	95	96	101
2	121	108	109	107	92	101	79
3	108	114	124	119	93	99	75
4	134	100	79	64	72	37	67
Totals ...	488	425	426	382	352	333	322
Means ...	122	106	107	96	88	83	81

The usual analysis of variance for a normal distribution gives the least significant difference between means at p=0·05 as 27. The same trend is seen in the yield figures as in the figures for dead beetles, but the significance is not so readily demonstrated as with the dead beetles. Thus aldrin was significantly better than the untreated control, Agrocide 3 applied with a rotary blower and Agrocide bait, and almost significantly better than Agrocide 3 with the fertiliser. Mergamma A and Agrocide 7 were nearly significantly better than the control.

Experiment No. 2.

This experiment, using treatments (1) to (4), inclusive, and (7), was laid down in the same way. The aldrin, however, was at half the strength, namely 3·6 oz. technical aldrin per acre. Plots were laid out for treatments (5) and (6) and insects counted on them, but the treatments were not applied and these plots were therefore additional controls. The kill began at an early stage in this experiment too, but in the first few days very many birds (storks, crows, etc.) visited the plots and picked up many of the dead and dying beetles. Guards were then placed on the plots during all daylight hours, and the numbers of dead beetles recovered increased in consequence. Later, the plots were flooded as a result of abnormal rain and the experiment had to be abandoned before harvesting. The birds did not collect the insects evenly over all the plots, but this is only one of the various sources of error with which the statistical analysis is designed to deal, and the results of the experiment are not without value, since they partly confirm those of experiment No. 1. The numbers of dead beetles collected are given in the following table.

Plots	Aldrin	Mergamma A	Agrocide 7	Agrocide 3 with fertiliser	Untreated	Untreated	Untreated
	1	2	3	4	5	6	7
1	195	275	90	146	5	5	5
2	77	165	106	37	15	2	3
3	84	161	76	51	2	3	3
4	73	111	117	69	1	3	11
Totals ...	429	712	389	303	23	13	22
Transformed variates, log. (1+x).	7·98	8·92	7·95	7·31	2·76	2·46	3·06

The figures were transformed as for experiment No. 1. The least significant difference at p=0·05 is 1·33. All treatments are therefore significantly better than the controls. Mergamma A is significantly better than Agrocide 3, but there is no significant difference between aldrin, Mergamma A and Agrocide 7, or between aldrin, Agrocide 7 and Agrocide 3. In this experiment, the order of aldrin and Mergamma A was reversed, and since the aldrin was at half the strength, this may be considered to give a useful indication of the strength at which it should be applied.

Summary.

Insecticidal treatments against *Heteronychus consimilis* Kolbe, a serious pest of wheat in Kenya, killed large numbers of adults and markedly reduced the damage done by them. Subsequent damage by larvae was prevented.

The most effective of the treatments tested were aldrin at 7·2 oz. per acre applied with the fertiliser, BHC in the form of Mergamma A applied as a seed dressing at 3¼ oz. per acre, and BHC in the form of Agrocide 7 applied as a seed dressing at 3¼ lb. per acre. The best treatments resulted in considerable increases in yield and gave promise of effective practical control on a large scale.

Acknowledgements.

Thanks are due to Messrs. Shell Chemicals Distributing Company (Africa) Limited for supplying the aldrin used, and to Messrs. Plant Protection Ltd. and their agents, Messrs. African Explosives and Chemical Industries (East Africa) Ltd., for supplying the BHC products used. The authors are also indebted to Mr. A. Lacey of the latter company for his interest in the work, to Mr. J. T. T. Schouten of the Agricultural Department for local assistance with various aspects of it, and particularly to the farmers on whose land experiments were conducted, namely Mr. S. J. Odendaal and Mr. R. K. S. Hendry, whose most helpful co-operation was much appreciated.

THE RECORDED DISTRIBUTION OF *ORNITHODOROS MOUBATA* (MURRAY) (ACARINA).

By H. S. Leeson.

London School of Hygiene and Tropical Medicine.

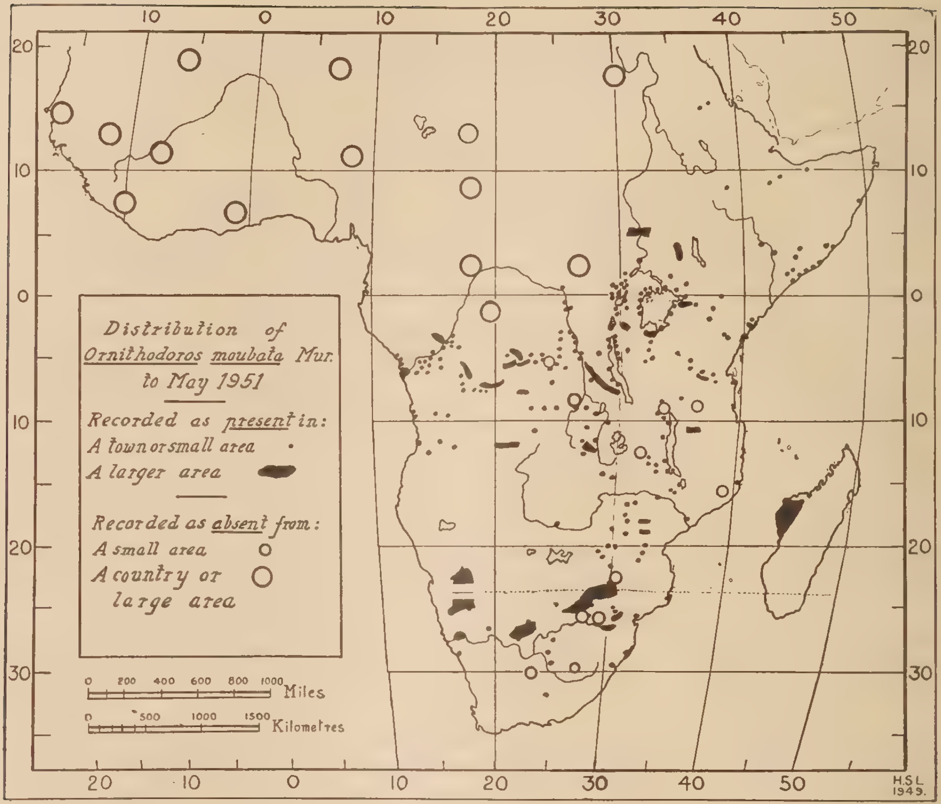
The tick, *Ornithodoros moubata*, was named by Murray in 1877 as *Argas moubata* ; his specimens came from Angola (Portuguese West Africa), where twenty years earlier, Livingstone had noticed that such ticks were common in native huts ; but Murray's description was " quite useless " (Nuttall & others, 1908) and it was Pocock (1900) who first published a recognizable description of the species and distinguished between *O. moubata* and *O. savignyi* (Audouin).

Africans had for a long time attributed relapsing fever or " tick fever " to this tick and, in 1904, Ross and Milne demonstrated that *O. moubata* is the vector of *Spirochaeta duttoni* ; this was later confirmed by Dutton and Todd (1905).

O. moubata seems to have spread westward and southward from the arid regions of East Africa so that now it occurs south of the equator from the east coast to the west coast. The most northerly record comes from Eritrea (Stella, 1940) and the most southerly from Graaf-Reinet and an adjoining village in South Africa (S. Afr. Inst. med. Res., 1945). The tick has been found at altitudes from sea-level to 3,000 metres (9,800 feet), the highest altitude recorded being at Lubero in the Belgian Congo (Flamand, 1928). The first case of relapsing fever on the high veldt of the Transvaal was recorded in 1939 from Kinross when the tick was also found (De Meillon, 1940).

Definite records of the occurrence of *O. moubata* in certain areas of the following countries have appeared in the literature to May 1951 : Abyssinia, Anglo-Egyptian Sudan (south), Angola, Bechuanaland, Belgian Congo, British Somaliland, Eritrea, French Somaliland, Italian Somaliland, Kenya, Middle Congo (south), Mozambique, Northern Rhodesia, Nyasaland, Southern Rhodesia, South West Africa, Tanganyika, Uganda, Union of South Africa. Outside the mainland *O. moubata* occurs in Madagascar, near the north-west coast (Le Gall, 1943 ; Néel & others, 1949).

Certain aspects of the distribution as shown on the map (fig. 1) require explanation. Nuttall & others (1908) quoting Brumpt (1901) say that *O. moubata* is " common in prisons in Zanzibar " and that this " locality is mapped by Dutton and Todd " (1905b) ; Merriman (1911) also shows Zanzibar on his map of distribution, repeated by Hindle (1911), but Aders (1914) states that *O. moubata* is unknown in Zanzibar, and among a list of 13 ticks occurring in Zanzibar (Aders, 1917), there is no Argasid. Since nothing further has been reported from this locality the record has been omitted from the present map. Egypt and an area south of Lake Chad were quoted by Nuttall & others (1908) from Neumann (1901) but it seems advisable to drop them from the records ; they concern one specimen from each place named by Neumann *Ornithodoros savignyi* var. *caecus*, a variety of *O. savignyi* without eyes, and considered by Nuttall to be a synonym of *O. moubata*, but it has not since been reported from these places. In fact, Le Gac (1931) in his detailed account of an outbreak of relapsing fever in Ouadai (Tchad) says a careful search for *O. moubata* failed to discover any. Records of var. *caecus* from other parts of Africa do not affect the issue. Before World War II, Italian workers (Franchini, 1935) claimed to have identified three possible tick vectors of relapsing fever in Cyrenaica one of which was *O. moubata*. Some years later, Coghill, Lawrence and Ballantine (1947) reported that Adler and Theodor had examined specimens of ticks sent to them from Tobruk


10
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Distribution of Ornithodoros moubata Mur. to May 1951
Recorded as present in:
A town or small area •
A larger area
Recorded as absent from:
A small area ○
A country or large area ◯
0 200 400 600 800 1000 Miles
0 500 1000 1500 Kilometres
20
10
0
10
20
30
40
50
H.S.L. 1949.

Fig. 1.

during the war and had identified them as *O. tholozani* (Lab. & Mégn.), a species not included in Franchini's list. This was the first record of this species being found west of Cyprus, and it is possible that Franchini's record of *O. moubata* was based on a misidentification ; it has therefore not been entered on the map. Commenting on their search of the literature relating to relapsing fever in Italian North Africa, Coghill, Lawrence and Ballantine remark that they are left " with a rather confused picture as to the vectors responsible." I have abstracted the Eritrean and Somaliland records from Italian and English papers, but chiefly from Stella (1940) who gives a list of 48 species and varieties of ticks (including *O. moubata* and *O. savignyi*) from Abyssinia, Eritrea, Somalia, British and French Somaliland and names the places where they were found. These localities are therefore retained and marked on the map.

In constructing the map, the recorded localities were first plotted on to a large scale map and then transferred to the small one reproduced here (fig. 1). It was then apparent that the distribution of *O. moubata* had a linear formation which seemed to follow the lines of communication, rivers, roads, tracks and railways. This then suggested that the tick was probably carried about from place to place by man and left, either purposely or accidentally, at intervals along these routes. The possibility that the tick was carried intentionally is supported by statements made by some authors, for instance, Ordman (1941), quoting from a personal communication, says : " In Nyasaland the Angoni take a supply of ticks with them when they are likely to be away from home for a long period." Again, speaking of South Africa he says : " It is known by some of the older European residents that the natives of Matala's tribe carry ticks with them in this way " ; and Phipps (1950) writing on *Ornithodoros* in Tanganyika says : " The Warundi, when they leave their own country to work elsewhere, often carry a few specimens of *O. moubata* in a match box and allow them to feed on themselves in order not to lose their immunity " to relapsing fever.

The tick has been searched for and has been reported as absent from parts of the above countries : for example, Nawalia district, Northern Rhodesia (Kinghorn, Yorke & Lloyd, 1913) ; the neighbourhood of the Rovuma river, Songea district, Tanganyika (Beck & Weck, 1913) ; Alto Mólôcuê, Mozambique (McFarlane, 1916) ; the dense humid forests of the Lower Congo (Rodhain, 1920) ; certain villages on the banks of the Congo river (Van den Branden, 1924) ; a volcanic area in the Belgian Congo (van Saceghem, 1923) ; generally south of the Orange river, South Africa (Bequaert, 1930) ; the Witwatersrand and other places in the Transvaal (Ordman, 1939, 1941). Some of the districts mentioned in earlier records may of course now be invaded but the tick appears to be absent from Algeria, the northern part of the Anglo-Egyptian Sudan, all French Equatorial Africa, except the extreme south, French West Africa, Gold Coast, Libya, Morocco, Nigeria, Tunisia ; in other words, from all the countries in Africa north of the Equator and west of longitude 30° East.

Records have been abstracted from original papers, the *Review of Applied Entomology*, the *Tropical Diseases Bulletin*, and the *Zoological Record.* I am particularly grateful for the assistance of Messrs. C. V. Meeser, W. D. Alves and J. A. Whellan who provided the Southern Rhodesia records.

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IMPROVEMENT OF THE RESIDUAL TOXICITY OF DDT SOLUTIONS BY THE ADDITION OF COUMARONE RESIN.

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It is a well-known fact that for special purposes DDT is often used in the form of a solution. Such preparations are, for instance, used for spraying water surfaces against the larvae of malaria mosquitos, for low-volume sprays on agricultural crops, for impregnating textiles and packing material, and for spraying stables and dwellings against flies, mosquitos, bugs, etc.

The solvent used is generally a light oil fraction, in particular the kerosene fraction. When any unpleasant odour has to be avoided, as when dwellings are treated, the DDT is dissolved in aromatic-free kerosene. This aromatic-free kerosene, however, dissolves considerably less DDT than the ordinary commercial kerosene, so that the required percentage of DDT (5 per cent.) cannot be kept in solution without adding auxiliary solvents. Various drawbacks are attached to these auxiliary solvents, however. In the first place they have a strong smell or an irritating effect on the mucous membranes and the solubility of the DDT, when stored at low temperatures, is reduced. Finally, after a DDT solution in kerosene evaporates, a very coarsely crystalline residue of long, needle-shaped crystals is left. From the literature it is known (Barnes, 1945 ; Doner, 1947 ; Woodruff & Turner, 1947) that the toxicity of DDT residues is closely dependent on particle size, toxicity increasing as the latter decreases.

Fine crystalline residues of DDT may be produced after evaporation of many solvents more volatile than kerosene, such as acetone or xylene, in which the crystals have only a short time to develop in the evaporating liquid. Many solvents of such high volatility are, however, not suitable for practical purposes because of the danger of the formation of poisonous vapours or explosive mixtures with air.

The object of the present investigation was therefore :—

1. To find means of obtaining a DDT deposit of crystals of smaller particle size, retaining kerosene as the solvent, thereby enhancing the activity.

2. To find out whether the higher toxicity thus obtained is such as to permit the DDT content in the solution to be reduced without the loss of effectiveness. This would remove the risk of crystallization during storage at low temperatures and make the addition of special solvents unnecessary.

Materials and Methods.

The biological material used was the ordinary house-fly, *Musca domestica* L. The results of the investigation were checked on the yellow fever mosquito, *Aëdes aegypti* (L.).

With the aid of a vertical spraying apparatus (ten Houten & Kraak, 1949), accurate doses of 250 mg. liquid per 100 cm.^{2} are sprayed on to small glass surfaces. These glasses are placed to dry for some days on wooden plates, protected from dust, until all the solvent has evaporated. Then these surfaces are made into test boxes with the aid of adhesive plaster. The boxes measure 3×3×8 cm., so the space is too small to permit of flight. All the inner surfaces having been sprayed, continuous contact of the flies with the insecticide is ensured during the period of exposure.

About 20 flies are then placed in the boxes and exposed for 30 sec. to the toxic effect of the residue. Apart from a few modifications, this method resembles in principle that generally applied in U.S.A. for testing the insecticidal effect of dry residues (Fay & others, 1947 ; Doner & Anderson, 1947 ; Block, 1948).

After exposure, the flies are quickly transferred to observation bottles, on the bottom of which cotton wool moistened with a solution of sugar is laid, and the knockdown percentage after various periods ($\frac{1}{4}$ to 4 hours) is recorded. Plotting the knockdown percentage against time after exposure, a curve in the shape of a flattened " S " is obtained, which is the steeper as the residue is more highly toxic. Except in one test in which very small quantities of DDT had been sprayed, the 24-hour or 48-hour mortality proved unsuitable as a criterion for toxicity, as it invariably amounted to 90 to 100 per cent. with the usual dosage.

When the empty boxes are left closed and unused in the dark without any further treatment, the toxic effect of the residue remains unchanged. The mortality of house-flies 48 hours after contact for 30 seconds with residues of 0·25 mg. DDT/100 cm.^{2} was 83, 79 and 83 per cent. when the ages of the residues tested for the first time were 21, 150 and 217 days, respectively.

When the same residues are tested at regular intervals, changes in toxicity are observed as a result of mechanical crumbling and absorption of DDT by the action of the flies crawling over the surface. On the whole, toxicity decreases in proportion to the frequency with which the residue has been tested, and the rate of this deterioration provides a measure of the relative duration of effectiveness of different residues.

Experiments.

The considerable difference in toxicity between fine and coarse crystalline residues can easily be demonstrated with residues of DDT solutions in kerosene and xylene, respectively. The former are coarsely crystalline (length of crystals about 2,000 μ), the latter being fine (length of crystals about 100 μ). Upon testing these residues (6·25 mg. DDT/100 cm.^{2}), the knockdown after two hours' exposure was found to be 29 and 84 per cent. respectively.

In order to obtain finely crystalline residues from DDT solutions in kerosene, very small quantities of coumarone resin (hereafter referred to as resin) were added to the kerosene. It was already known (West & Campbell, 1946) that insecticide paints containing equal quantities of DDT and resin are highly effective. These paints contain a supersaturated solution of DDT in resin and the DDT crystallizes into micro-crystals when the paint dries. It was now found that resin also greatly affects the crystallization of DDT in quite a different way, even in very low concentrations. As little resin as 1 part to 100 parts DDT causes a marked reduction in the size of the crystals. If the resin concentration is increased, there is a corresponding reduction in the size of the crystals (from about 2,000 μ to about 200 μ) until maximum reduction is reached at a resin DDT ratio between 1 : 10 and 1 : 2. Beyond this point the DDT is enclosed in resin, and crystals occur only sporadically.

In testing the toxicity of such DDT/resin residues it might therefore be expected that the effectiveness would be determined by the DDT/resin ratio and not the absolute content of resin. This indeed proved to be the case for, when 0·5 per cent. resin was added to solutions of 4, 2 and 1 per cent. DDT in kerosene, a considerable increase in residual toxicity was produced with 4 per cent. DDT, practically no change with 2 per cent. DDT, and a strong reduction with 1 per cent. DDT (figs. 1, 2 and 3).

These results show that resin may have either a synergistic effect (resulting from the reduction in crystal size) or an antagonistic effect (resulting from the masking

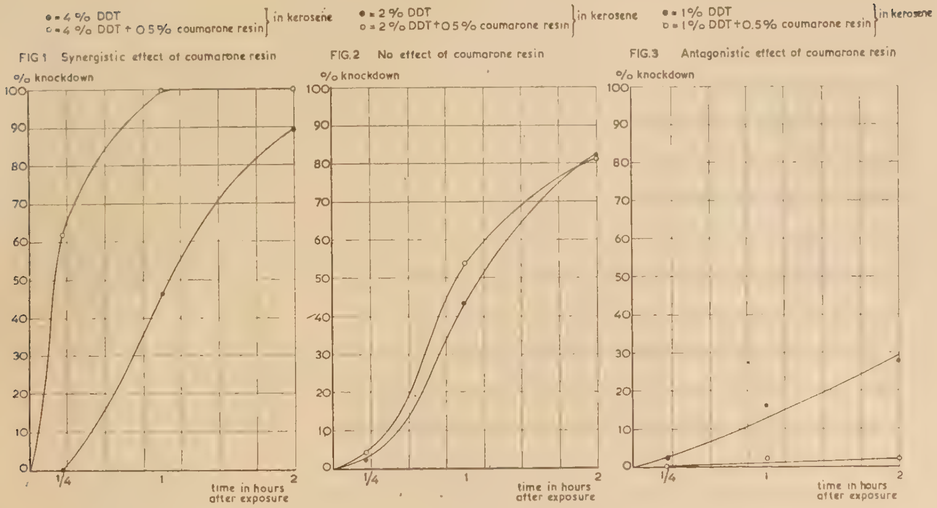


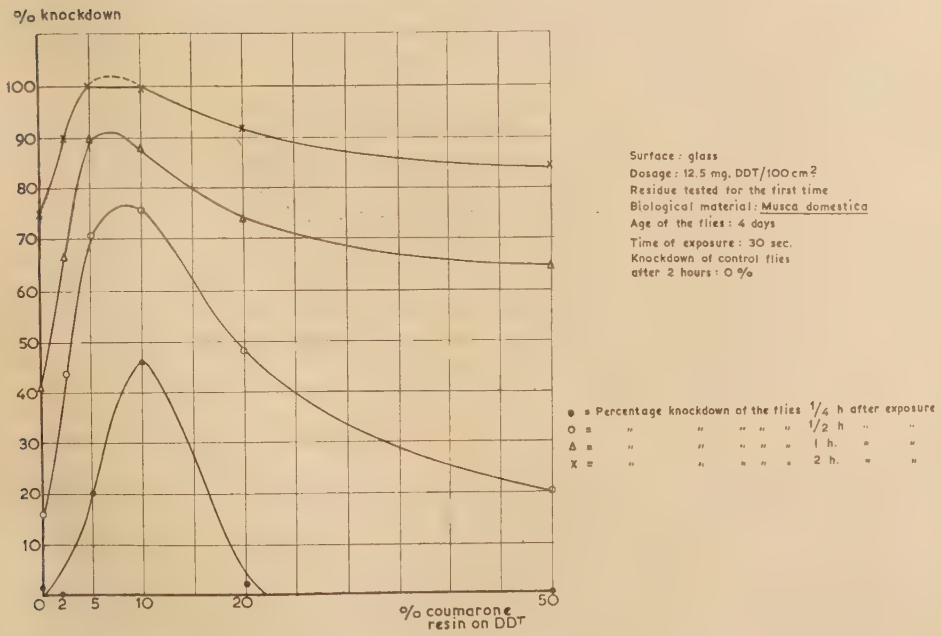
FIG. 1 Synergistic effect of coumarone resin

FIG. 2 No effect of coumarone resin

FIG. 3 Antagonistic effect of coumarone resin

Dosage of the spray liquid: 250 mg./100 cm.^{2}
Surface glass
Residue tested for the first time
Biological material: Musca domestica
Age of the flies 2 days
Time of exposure: 30 sec
Knockdown of control flies after 2 hours: 0 %

Figs. 1–3.—Influence of coumarone resin on the toxicity of DDT residues.



Surface: glass
Dosage: 12.5 mg. DDT/100 cm^2
Residue tested for the first time
Biological material: Musca domestica
Age of the flies: 4 days
Time of exposure: 30 sec.
Knockdown of control flies after 2 hours: 0 %

Fig. 4.—Relation between residual toxicity and coumarone resin/DDT ratio.

of the crystals) upon the toxicity of crystalline DDT residues, depending on the resin/DDT ratio. Beyond a certain ratio, a synergistic effect changes into an antagonistic one. It is therefore desirable to determine the optimum ratio.

To this end determinations were made of the toxicity of residues from 5 per cent. DDT solutions in kerosene, without resin, and with concentrations of resin varying from 0·1 to 2 per cent. It was found that the residual toxicity reached a maximum at about 0·5 per cent. resin content, in other words when the resin/DDT ratio was about 1 : 10. Results are shown in fig. 4.

A similar relation between toxicity and resin/DDT ratio was also found at the far lower DDT concentrations of 1 per cent. (Table I).

TABLE I.

Knockdown percentage of house-flies one hour after 30 sec. contact with DDT residues with resin on glass deposit tested for the first time.

	Percentage of resin added to a 1 per cent. DDT solution in kerosene (250 mg. sol./100 cm.^{2})			Control
	0·03	0·1	0·2	
Percentage knockdown	20	70	29	0

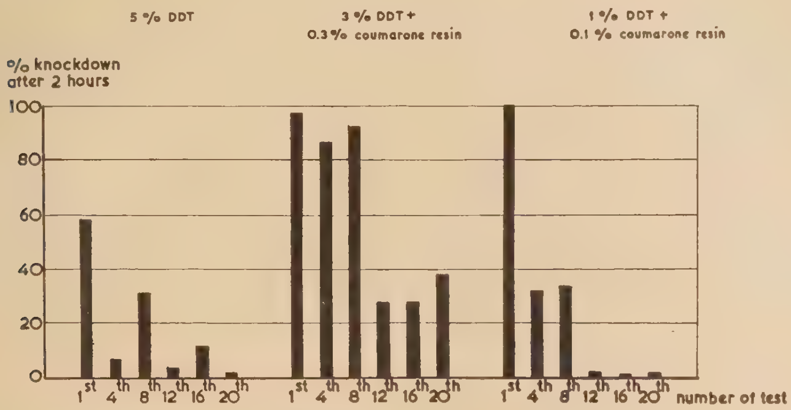
The next problem was to ascertain whether resin was able to increase the toxicity of residues of DDT solutions in kerosene to such an extent that the DDT content could be reduced. The initial toxicity of DDT residues with various DDT contents, with and without resin, was determined and it was found that the synergistic effect of resin was so strong that even residues of a 1 per cent. DDT+0·1 per cent. resin solution in kerosene when tested for the first time were more toxic than residues of a 5 per cent. DDT solution without resin (Table II).

TABLE II.

Knockdown percentage of house-flies one hour after 30 sec. contact with DDT residues with and without resin, on glass deposits tested for the first time (250 mg. sol./100 cm^2.).

Per cent. DDT	Per cent. resin			
	0	0·1	0·3	0·5
5	12			90
3	2		82	
1	2	87		
Control ...	0	0	0	0

To determine how far the DDT content of the usual residual sprays with a kerosene base could be reduced by the addition of resin without affecting the residual effect, the persistency was determined, especially of residues on glass from a 5 per cent. DDT solution without resin and of those from 3 per cent. and 1 per cent. DDT solutions with resin. The activity of these residues was tested several times at intervals of 1–2 weeks. The superiority of residues from 1 per cent. DDT+0·1 per cent. resin solutions over residues from 5 per cent. DDT solutions without resin was maintained for 7 tests (69 days) only ; after this period, the residues from the 5 per cent. DDT solutions without resin were the more toxic. This shows that the resin cannot permanently compensate for a reduction in DDT content from 5 per cent. to 1 per cent. On the other hand, the 3 per cent. DDT+0·3 per cent. resin residues showed distinctly higher toxicity to house-flies throughout the experiment (20 tests in 244 days) than the 5 per cent. DDT residues without resin. The results are shown in fig. 5.



Surface : glass
Dosage of the spray liquid : 250 mg./100 cm²
Biological material : Musca domestica
Age of the flies : 3 days
Time of exposure : 30 sec.
Knockdown of control flies after 2 hours : 0 %

Fig. 5.—Comparison of the toxicity of DDT-residues with and without coumarone resin in successive tests.

These data all relate to the residual effect on glass, because this material is pre-eminently suitable for laboratory investigations into the residual effect of insecticides : it is not porous, its surface is even and the crystallization of the active material is easily perceptible. However, it is not the surface to which residual

TABLE III.

Percentage knockdown of house-flies ½ hour after 30 sec. contact with DDT residues with and without resin on various surfaces tested for the first time.

Surface	Spray liquid containing			Control
	5 per cent. DDT	5 per cent. DDT +0·5 per cent. resin	3 per cent. DDT +0·3 per cent. resin	
Glass	0	31	33	0
Iron	0	42	27	0
Unpainted wood ...	2	49	28	0
Paper	0	18	36	0
Cotton cloth	8	45	43	0
Mortar	0	0	2	0
Mortar* (4 hours after contact)	10	81	83	0

*Owing to the penetration of DDT solutions into very porous material, such as mortar, the effect on this material is only slight and therefore the knockdown percentages 4 hours after exposure have also been included.

sprays will be most applied in actual practice. It was therefore of importance to determine the effect of resin on the residual toxicity on other surfaces. Consequently the residual effect of a 5 per cent. DDT solution with and without 0·5 per cent. resin and a 3 per cent. DDT solution with 0·3 per cent. resin was studied on iron, unpainted wood, paper (weight 175 g/m^2), cotton cloth and mortar (compared with glass).

The experiments showed that the toxicity of the residue was in all cases considerably increased by the addition of resin to the DDT solution in kerosene. On these surfaces also, residues from 3 per cent. DDT+0·3 per cent. resin solutions were more toxic than those from 5 per cent. DDT solutions without resin (Table III).

Check experiments with *Aëdes aegypti* showed also a very important increase in toxicity by the addition of resin to the DDT solution.

Thus, it has been found that the addition of small quantities of resin (1/10 of the DDT concentration) allows of a reduction in DDT content from 5 to 3 per cent., which latter percentage can be easily dissolved, even in refined kerosene, so that it does not recrystallize during storage at low temperatures, and auxiliary solvents can be omitted. Residues of such a DDT-resin solution have a microcrystalline structure and therefore a considerably greater toxicity and persistency than the coarsely-crystalline residues from sprays containing DDT without resin.

Summary.

An investigation was made into means of increasing the effectiveness of the usual DDT-containing residual sprays with a kerosene base.

The common house-fly, *Musca domestica*, was used as biological material.

It was found that there exists a distinct relationship between crystal size and residual toxicity. Finely crystalline residues from DDT solutions in volatile solvents, such as xylene, proved to be considerably more toxic than coarsely crystalline residues from DDT solutions in less volatile solvents, such as kerosene. Addition of small quantities of coumarone resin to a DDT solution in kerosene was found to reduce the size of the DDT crystals and to increase the toxicity considerably.

This synergistic effect increased with the resin concentration and reached a maximum when the concentration of the resin was about 10 per cent. that of the DDT. Above this concentration the effect decreased again, owing to the masking of the DDT crystals by the resin. At a resin/DDT ratio of 1 : 2 the resin was found to have an antagonistic effect and the residual toxicity dropped to below that of the corresponding solution without resin.

The residual effect of a 1 per cent. DDT+0·1 per cent. resin solution in kerosene was found to be even greater than that of an equal quantity of a 5 per cent. DDT solution without resin, but this superiority only lasted for 69 days, when the residue was tested at intervals of 1 to 2 weeks. Residues from a 3 per cent. DDT+0·3 per cent. resin solution in kerosene, however, were found to be permanently more toxic than those from a 5 per cent. DDT solution without resin. In other words, the addition of 0·3 per cent. resin allows the DDT content to be reduced from 5 to 3 per cent. These results not only apply to residues on glass, but also to those on other materials such as iron, unpainted wood, paper, cotton cloth and mortar, the surfaces of which are more like those which have to be sprayed in actual practice.

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THE EARLY STAGES OF BRITISH BITING MIDGES *CULICOIDES* LATREILLE (DIPTERA: CERATOPOGONIDAE) AND ALLIED GENERA.

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(PLATES XIV–XIX.)

Edwards (1939) has given a comprehensive account of the adults of most British species of *Culicoides*; but relatively little is known of the early stages, although Hill (1947) quotes a description of a larva and pupa of what is apparently *Culicoides* given by the Rev. W. Derham so long ago as 1712. In 1919 Goetghebuer described the larva of *C. pulicaris* (there is reason to believe that the larva so described was in fact not that of *C. pulicaris*—see p. 445): and in 1920 Carter, Ingram & Macfie produced their study of the Gold Coast Ceratopogonine midges. Descriptions of the early stages of European species are provided by Thienemann (1928), Mayer (1934), in a compilation by Lenz (1934) and by Hill (1947), who also made an exhaustive survey of the literature and drew attention to the scarcity of larval descriptions. The following table shows those European species, of which at least one of the early stages has been described, and the author of the description:—

	Larva	*Pupa*
C. circumscriptus Kieff.	Tokunaga (1937)	Tokunaga (1937)
C. cubitalis Edwards	Hill (1947)	Hill (1947)
C. halophilus Kieff.	—	Lenz (1934)
C. impunctatus Goet.	Hill (1947)	Hill (1947)
C. nubeculosus (Mg.)	Mayer (1934)	Mayer (1934)
	Lawson (1951)	Lawson (1951)
C. obsoletus (Mg.)	Hill (1947)	Hill (1947)
C. odibilis Austen	Hill (1947)	Hill (1947)
C. pallidicornis Kieff.	Hill (1947)	Hill (1947)
C. pictipennis (Staeger)	—	Thienemann (1928)
C. pulicaris (L.)	Goetghebuer (1919)	Rieth (1915)
	Thienemann (1928)	Thienemann (1928)
C. riethi Kieff.	Rieth (1915)	Rieth (1915)
	—	Thienemann (1928)
C. salinarius Kieff.	Rieth (1915)	Rieth (1915)
C. setosinervis Kieff.	Rieth (1915)	Rieth (1915)
C. stigmaticus Kieff.	Rieth (1915)	Rieth (1915)

Carter, Ingram & Macfie (1920) suggested that the "hypopharynx" of the larva might provide valuable taxonomic characters, but also pointed out that these structures cannot be properly examined *in situ*. The present work confirms this; the pharyngeal skeletons have been removed from the head capsule and examined from the ventral side under a one-twelfth oil-immersion objective. Such examination takes about an hour and, in consequence, is not applicable to quantitative field studies. Fortunately, it was found that the larvae of different species could be separated on the colour and size of the head capsule and the pigmentation of the thorax.

Previous descriptions of the larvae have not included a detailed study of the pharyngeal skeleton nor of the thoracic pigmentation, and, to this extent, are incomplete.

The available descriptions of the pupae are more satisfactory than those of the larvae, because the pupae show more conspicuous specific characters. It should be pointed out, however, that two features on which reliance has been placed—the operculum and the respiratory organ—vary to some extent from individual to individual, the range of variation being greater in some species than in others. In the case of at least two species, the ranges of variation of the respiratory organ overlap, thus making it impossible to distinguish these species on this character alone.

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Before describing our findings in detail, it will be useful to consider Hill's (1947) larval results.

Hill's Results (*1947*).

In her paper on the life-cycle of six British species of *Culicoides*, Hill (1947) records the measurements of the head capsules. Some of these agree very closely with those given here, but in others there are differences too large to be the result of experimental error (Table I).

TABLE I.

Comparison of Hill's (1947) measurements of *Culicoides* larval heads with those recorded in this paper.

(*a*)	(*b*)	(*c*)	(*d*)	(*e*)	(*f*)	(*g*)	(*h*)
				This paper			
Species	Instar No.	Head measurement	Hill 1947 μ	Mean μ	95% fiducial interval μ	Range μ	Difference (*d–e*) μ
C. odibilis	4	Length	190	190	±2	180–197	0
,, ,, ...	4	Breadth	132	137	±4	123–152	−5
C. pallidicornis ...	4	Length	200	199	±1	185–209	+1
,, ,, ...	4	Breadth	140	130	±1	115–143	+10
C. cubitalis	4	Length	180	166	±1	156–176	+14
,, ,, ...	4	Breadth	140	104	±1	98–115	+36
C. obsoletus	4	Length	217	170	±2	164–176	+47
,, ,, ...	4	Breadth	164	123	±2	115–131	+41
C. impunctatus ...	4	Length	233	235	±2	217–250	−2
,, ,, ...	3	,,	176	169	±1	156–180	+7
,, ,, ...	2	,,	133	118	±1	106–127	+15

It will be seen that there is good agreement between the two sets of figures for *C. odibilis*, *C. pallidicornis* and *C. impunctatus* (third and fourth instars) and practically no agreement on the head size of *C. obsoletus*, *C. cubitalis* and *C. impunctatus* (second instar). This variation rules out the possibility of there being a fixed error in either set of calculations, *e.g.*, incorrect calibration of the micrometer scale. Neither can the divergence be due to the measurements having been made between different parts of the head capsule, as this would affect only the length, and the discrepancies are equally large in the breadth. Moreover, Hill's figures for *C. obsoletus*, *C. cubitalis* and *C. impunctatus* (second instar) are outside the range of the material described here. Recently two new species, *C. pseudochiopterus* and *C. scoticus* have been described by Downes and Kettle (1952), the females of which are nearly indistinguishable from those of *C. obsoletus*, but which differ in the male genitalia. However, the larval heads of both these species are slightly smaller than that recorded here for *C. obsoletus*. In any case Hill recorded the male genitalia of her *C. obsoletus* as being identical with those figured by Edwards (1939) and Root and Hoffman (1937) and therefore Hill must have been dealing with *C. obsoletus*, *sensu stricto*, and not with either of its near relatives.

Hill gives the head lengths of second, third and fourth instar *C. impunctatus* as 133 μ, 176 μ and 233 μ respectively and points out that they fit a ratio of increase of 1·32 (p. 77). Later in the same paper she records the head length of the first instar as 76 μ (p. 90). If the head length of the first instar is 76 μ and the ratio of increase 1·32, then the second instar should have a head length of 76 μ × 1·32 = 100 μ but it has a head size of 133 μ according to Hill, which is equal to 76 μ × 1·75 (= 76 μ × 1·32 × 1·32). There are three possible explanations of this result. Firstly, the growth of the head capsule of *C. impunctatus* may not follow Dyar's Law. This seems unlikely in view of the observations on other species of the same genus, *C. truncorum* and *C. nubeculosus* (fig. 1). Secondly, there may be five instars with head lengths of 76 μ, 100 μ, 132 μ, 176 μ and 233 μ. This is highly improbable in so far as most dipterous larvae have four instars, even if one is reduced to a moult inside the puparium as in Muscid larvae. Lastly, the figures given by Hill may be incorrect.*

THE LARVAE.

Technique.

Most *Culicoides* larvae live at or near to the surface of wet soil in marshes or bogs and, to find them, samples 3 ins. diameter and 2–3 ins. deep were taken with a soil borer. Each sample was divided into fractions one inch thick, which were examined separately, the larvae being freed from the medium by means of the flotation technique of Ladell (1936). Each fraction was washed through two sieves, 10 and 20 mesh, by a strong jet of water and the filtrate then passed with the minimum of agitation, through an 80-mesh sieve. All the material retained on this last sieve was transferred to a small dish containing a very concentrated solution (25–33 per cent.) of magnesium sulphate (Sp. Gr. 1·15–1·20), the specific gravity of which was such that inorganic particles sank, while living and dead organic material floated.

Third and fourth instar *Culicoides* larvae were readily recognised by their active lashing swimming movements, but earlier instars tended to be more quiescent and to lie coiled on the surface of the fluid. Their removal was facilitated by the use of a low-power lens. It is believed that all the third and fourth and the majority of the

TABLE II.

Vertical distribution of *Culicoides* larvae.

Species	Instar No.	No. of larvae	% distribution				Breeding site
			0–1 in.	1–2 ins.	2–3 ins.	3 ins. +	
C. impunctatus	2	58	91	9	0	0	Luss.
,, ,, ...	3	210	85	12	3	0	
,, ,, ...	4	125	74	22	3	1	
C. truncorum	1	51	76	20	4	0	Luss.
,, ,, ...	2	232	75	18	5	2	
,, ,, ...	3	95	39	35	18	8	
,, ,, ...	4	116	34	34	24	8	
C. cubitalis	3	75	15	57	23	5	Drumchapel.
,, ,, ...	4	50	16	40	30	14	
C. pallidicornis... ...	3	22	72	5	18	5	Drumchapel.
C. obsoletus	4	16	75	19	6	0	Drumchapel + Luss.
C. albicans	3+4	27	4	30	44	22	Luss.
C. heliophilus	3+4	20	5	20	35	40	Luss.

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*Recently through the courtesy of Mr. Warwick Nicholas we have examined seven *C. cubitalis* larvae from Hill's site at Liverpool. Their heads averaged 164 μ long (Range 160–168) and 108 μ broad (Range 103–111), and thus agree with the measurements given in this paper.

first and second instars were recovered, since on those occasions when very young larvae were present they were found in large numbers (see *C. truncorum*, Table II). *Culicoides* larvae were apparently unaffected by immersion in magnesium sulphate solution for periods up to one hour.

The larva and adult of a species can be related in two ways. In the first method larvae, obtained from eggs laid by identified females, may be reared on a medium freed from other *Culicoides*. In the other method wild caught larvae, grouped on certain characters, can be kept until the adults emerge, in order to identify the species and to ensure that each group is homogeneous, containing one and only one species. The latter method was adopted here because of the difficulty of obtaining gravid females and the absence of detailed information as to the larval food.

In some early experiments grouped larvae were reared on sterilised soil ; but while some species, *e.g.*, *C. cubitalis* and *C. pallidicornis*, appeared to flourish under these conditions it was felt that the process of sterilisation had considerably altered the medium and might render it unsuitable to some species. Therefore small portions of unsterilised soil taken from the bottom of a core were used as rearing media. As the larval abundance decreases, usually rapidly, with increasing depth, the possibility of introducing extraneous *Culicoides* larvae with the medium was slight (see Table II). This was confirmed in practice by the almost complete absence of " contaminants ", but where these occurred they have been recorded.

For rearing, fourth-stage larvae were placed on a small piece of soil in a 3×1-in. tube closed with muslin gauze. The tubes were kept on a layer of wet cotton wool in a stoppered glass jar. This technique was very successful with full-grown fourth instars ; but adults were never obtained from third-stage larvae. This failure may be related to the exhaustion of the food supply because the larvae failed to grow although they often survived for long periods of time.

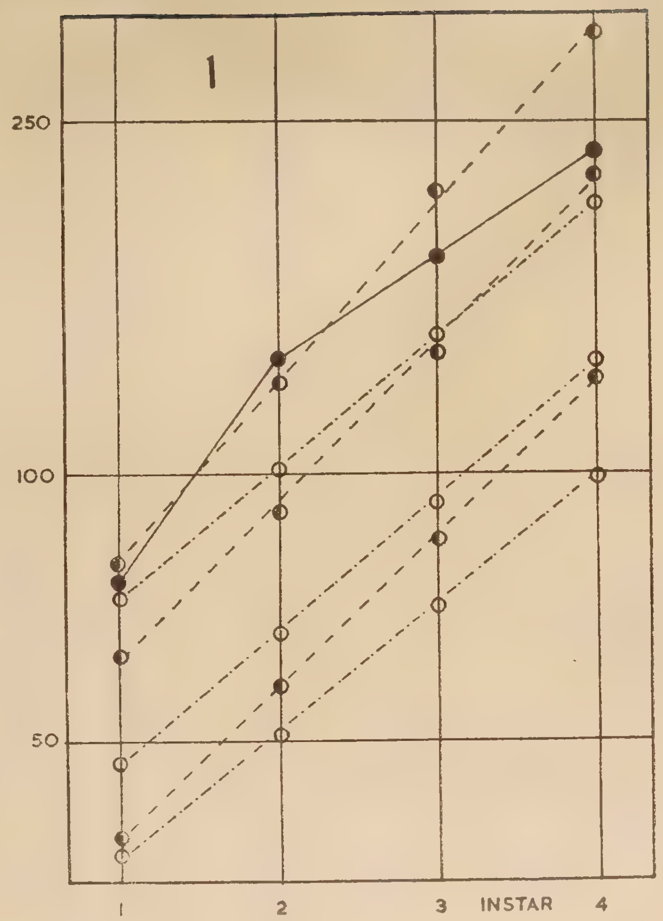
When related larval and pupal exuviae were required, individual larvae were kept in watch glasses in water with a small amount of material which had passed through a 100-mesh sieve. Otherwise, pupal exuviae were recovered from the larval tubes after the completion of adult emergence.

The following method of larval preservation was adopted and found satisfactory for retaining the characteristic pigment markings. Living larvae, dropped into hot water for a few seconds to render them immobile and relaxed, were preserved either in 70 per cent. alcohol or 2 per cent. formalin ; if left too long in hot water the markings are destroyed. Two per cent. formalin keeps the larvae more translucent than alcohol but tends to bleach out the pigment markings. Alcohol does not appear to suffer, from this disadvantage, as it was possible to examine specimens in the British Museum (Natural History) which had been preserved for 28 years and the markings were still recognisable. Of course, for histological and other specialised investigations the appropriate fixative should be used.

Explanation of Characters used in the Larval Key.

Recognition of fourth-instar larvae.

The first difficulty encountered when using the key is how to recognise a fourth-instar larva. There is no simple answer to this question, although there are a number of useful indications. Any larva showing signs of pupation is in the fourth instar. The first signs of this are the hollowing out of the mesothoracic and metathoracic paired lateral bodies (Pl. XVI) as they are pushed in by the growing imaginal buds. Much later the typical pupal structures, such as the respiratory horns and the caudal spines, become visible but by this time the larva is so distorted as to make identification very difficult (Pl. XVIII). In addition, the fat body in the abdomen of



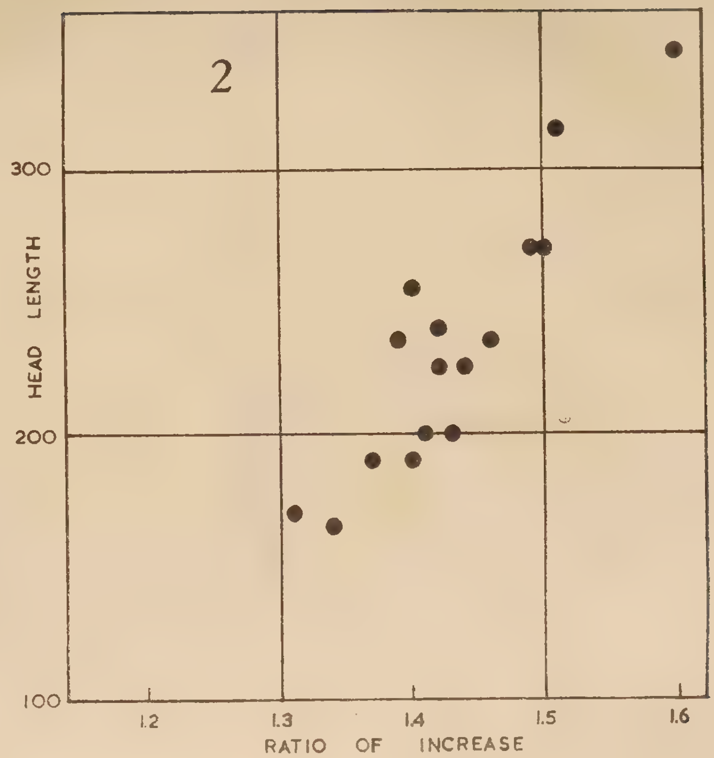
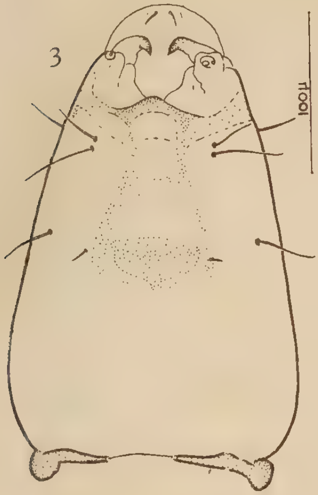
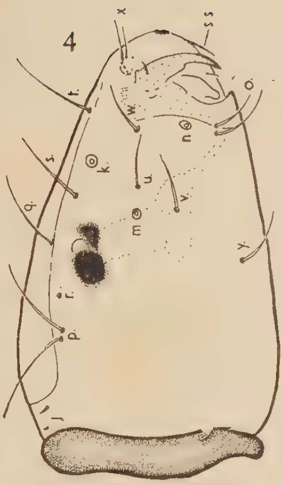
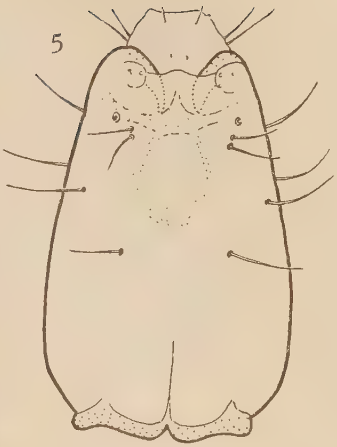


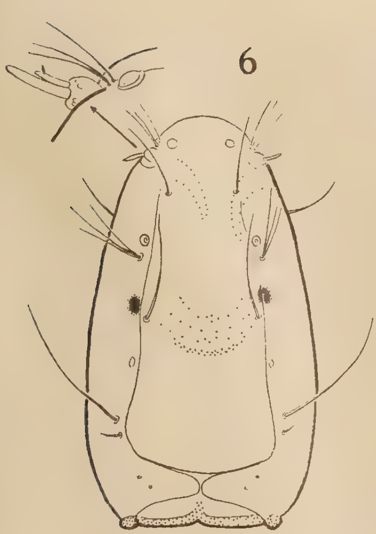
FIG. 1. Dyar's law and the head measurements of *C. nubeculosus* (half-closed circles and broken lines), *C. truncorum* (open circles and dash-dot lines) and *C. impunctatus* (closed circles and continuous lines). The upper, middle and lower lines of *C. nubeculosus* and *C. truncorum* represent head length, head breadth and oral ring breadth respectively. The measurements are in μ on a logarithmic scale. The data for *C. impunctatus* are taken from Hill (1947).

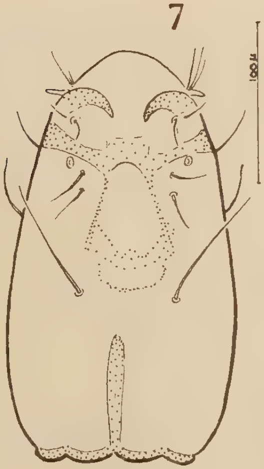
FIG. 2. The ratio of increase in head length from 3rd to 4th instar *Culicoides* plotted against the head length in μ of the 4th instar.











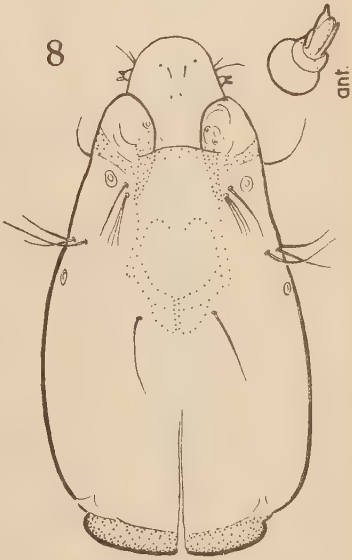


Fig. 3. *C. riethi*: ventral view of the head of the larva.

Fig. 4. *C. stigma*: lateral view of the head of the larva (s.s., setiform sensilla).

Fig. 5. *C. halophilus*: ventral view of head of the larva.

Fig. 6. *Ceratopogon* (*Isohelea*): dorsal view of the head of the larva and the antenna.

Fig. 7. *Ceratopogon* (*Isohelea*): ventral view of the head of the larva.

Fig. 8. *Stilobezzia ochracea*: ventral view of the head of the larva; dorsal view of the antenna.

a fourth-instar larva is very strongly developed so that the opaque grey abdomen contrasts markedly with the translucent thorax. Any larva with a head longer than 250 μ is in the fourth instar. The longest third-instar head measured so far belonged to a larva of *C. nubeculosus* Form *B* with a head length of 226 μ.

It is usually not difficult to recognise different instars of the same species and from these an estimate can be made of the ratio of increase in head length from instar to instar. In view of the fact that the head length of a first instar larva is usually between 70 μ and 80 μ and always under 90 μ, the instar numbers of the two unknown stages can be correctly assigned. For example, in a larval sample there appear to be two instars of a species. The larger larvae (X) have a mean head length of 203 μ and the smaller larvae (Y) have a mean head length of 144 μ. Therefore (r) the ratio of increase ($=X/Y$) is equal to $203/144=1{\cdot}41$. Since there are only four instars and the head lengths of the first is between 70 μ and 80 μ then X and Y are either the third and second instars or the fourth and third instars. If X is the third instar, then X/r^2 should be between 70 μ and 80 μ ; and if X is the fourth instar then X/r^3 should be between 70 μ and 80 μ. In fact $X/r^2=203/1{\cdot}41^2=102$ μ and $X/r^3=203/1{\cdot}41^3=72$ μ. Therefore X is the fourth instar and Y the third.

This calculation has been applied to the measurements given in Table III provided that five or more larvae have been measured in each instar. The estimated first-instar head lengths range from 68 μ to 93 μ and if those species whose fourth-instar head lengths exceeded 250 μ were excluded the range was from 68 μ to 88 μ. It was interesting to note that the ratio of increase was positively correlated with the size of the larval head (fig. 2).

Head.

The size and colour of the head is characteristic for all species. Most have either pale yellow heads (*C. cubitalis*, *C. albicans*, *C. heliophilus*) or amber heads (*C. obsoletus*, *C. cunctans* and *C. pulicaris* and its allies), but in a few examples the head colour is specific. Thus the larvae of *C. impunctatus* are readily recognised by their peculiarly muddy brown heads and those of *Stilobezzia* spp. by their dark chocolate brown heads.

The head size has been represented by three measurements—length, breadth and width of the oral ring. The *head length* is measured along the mid-dorsal line, from the hind border of the collar (post-occipital ridge) to the front edge of the translucent labrum (the ventral measurement is slightly larger). The post-occipital ridge or collar is a narrow transverse band forming the posterior border of the head capsule. Usually it becomes even narrower in the mid-dorsal line, but in some species, notably *C. nubeculosus* and its allies, it remains relatively broad and is turned forwards. In these species the posterior limit of the measurement is taken as the point of intersection of the mid-dorsal line and a line joining the inner margins of the collar before it is turned forwards. If the measurement is taken from the outer margins of the collar the head length is increased by about 10 μ. The *head breadth* is measured at the widest part of the head, usually in the posterior third. The *width of the oral ring* is measured along the hind border of this structure—the sub-genal band. The *head ratio* is the ratio of the head length to the head breadth.

In each species the head size is normally distributed and can be represented by the expression $x+s$ where $x=$ the mean and $s=$ the standard deviation of the population from the mean. Since the distribution is normal, two-thirds of the population will have head sizes ranging from $x-s$ to $x+s$. In Table III it will be seen that the values of s are small, indicating considerable uniformity in head size among larvae of the same species and instar. This property makes the larval head size a most useful specific character.

It has been suggested (Kettle, 1948) that Dyar's Law is a special case of the more general conception that the relative sizes of organs are determined by growth partition

TABLE III.

Mean head size of third- and fourth-instar *Culicoides* larvae together with the population's standard deviation from the mean.

		nubeculosus Form A		*nubeculosus* Form B	*riethi*	*stigma*
		Dorset	Ayrshire			
Fourth instar	H.L. ...	315 ±10	359 ±10	347 ±11	271 ±11	268± 8
	H.B. ...	217 ±12	222 ± 8	224 ± 8	178 ± 7	166 ± 5
	O.R.B.	128 ± 5	137 ± 5	141 ± 4	117 ± 2	101 ± 3
	H.R. ...	1·45± 0·08	1·57± 0·05	1·55± 0·05	1·52± 0·05	1·62± 0·05
	No. ...	21	10	11	5	21
Third instar	H.L. ...	209 ± 6		214 ± 8		180 ± 3
	H.B. ...	137 ± 6		134 ± 5		113 ± 5
	O.R.B.	84 ± 3		83 ± 5		72 ± 3
	H.R. ...	1·52± 0·05		1·59± 0·09		1·63± 0·07
	No. ...	20		13		9

		vexans	*albicans*	*truncorum***	*fascipennis*	*pallidicornis*
Fourth instar	H.L. ...	267 ± 5	268 ± 7	203 ± 7	247 ± 5	199 ± 5
	H.B. ...	186 ± 4	155 ± 4	134 ± 7	164 ± 6	130 ± 5
	O.R.B.	136 ± 4	117 ± 4	98 ± 4	115 ± 4	93 ± 3
	H.R. ...	1·43± 0·04	1·75± 0·05	1·52± 0·08	1·51± 0·06	1·53± 0·05
	No. ...	20	14	100	26	70
Third instar	H.L. ...		179 ± 6	144 ± 5	156	139 ± 5
	H.B. ...		103 ± 2	93 ± 5	96	92 ± 4
	O.R.B.		80 ± 2	71 ± 3	76	67 ± 2
	H.R. ...		1·75±0·07	1·55±0·08	1·62	1·51± 0·05
	No. ...		22	80	2	22

		cubitalis	*pictipennis*	*salinarius**	*circumscriptus*	*odibilis*
Fourth instar	H.L. ...	166 ± 4	243 ± 7	228 ± 6	234 ± 7	190 ± 4
	H.B. ...	104 ± 4	148 ± 5	157 ± 5	164 ± 7	137 ± 8
	O.R.B.	74 ± 3	109 ± 3	108 ± 2	111 ± 4	86 ± 3
	H.R. ...	1·60± 0·06	1·64± 0·06	1·45± 0·04	1·42± 0·06	1·39± 0·07
	No. ...	47	13	44	23	24
Third instar	H.L. ...	124 ± 5		158 ± 4		139 ± 4
	H.B. ...	77 ± 3		109 ± 4		90 ± 3
	O.R.B.	55 ± 2		72 ± 2		63 ± 2
	H.R. ...	1·63± 0·06		1·45± 0·04		1·54± 0·06
	No. ...	115		24		25

		*maritimus**	*simulator*	*heliophilus*	*cunctans*	*lupicaris*
Fourth instar	H.L. ...	225 ± 7	205	191 ± 6	230 ± 7	322 ± 9
	H.B. ...	140 ± 6	148	115 ± 5	158 ± 7	192 ± 6
	O.R.B.	105 ± 4	98	85 ± 5	108 ± 5	123 ± 4
	H.R. ...	1·61± 0·07	1·39	1·66± 0·06	1·45± 0·06	1·68± 0·06
	No. ...	30	1	28	16	11
Third instar	H.L. ...	159 ± 6		136 ± 3		208 ± 7
	H.B. ...	96 ± 4		80 ± 2		125 ± 2
	O.R.B.	75 ± 3		62 ± 2		84 ± 2
	H.R. ...	1·66± 0·07		1·69± 0·07		1·67± 0·07
	No. ...	31		11		4

TABLE III *cont.*

		grisescens	*delta*	*pulicaris*	*punctatus*	*halophilus*
Fourth instar	H.L. ...	294 ± 7	278 ±13	256 ± 9	234 ± 5	242 ±12
	H.B. ...	180 ± 5	173 ± 9	168 ± 6	155 ± 6	163 ± 7
	O.R.B.	137 ± 4	116 ± 3	112 ± 4	106 ± 4	109 ± 3
	H.R. ...	1·63 ± 0·04	1·61 ± 0·10	1·53 ± 0·07	1·51 ± 0·06	1·48 ± 0·08
	No. ...	6	6	97	47	31
Third instar	H.L. ...			183 ± 3	160 ± 5	170 ± 6
	H.B. ...			116 ± 5	104 ± 5	109 ± 5
	O.R.B.			80 ± 3	78 ± 2	80 ± 2
	H.R. ...			1·57 ± 0·07	1·55 ± 0·09	1·56 ± 0·07
	No. ...			16	37	12

		*impunctatus**	*obsoletus*	*scoticus*	*chiopterus*	*pseudo-chiopterus*
Fourth instar	H.L. ...	235 ± 8	170 ± 4	151	115 ± 5	163 ± 7
	H.B. ...	147 ± 5	123 ± 4	119	99 ± 4	122 ± 3
	O.R.B.	105 ± 4	92 ± 4	72	61 ± 2	80 ± 3
	H.R. ...	1·60 ± 0·07	1·38 ± 0·05	1·27	1·16 ± 0·05	1·33 ± 0·03
	No. ...	100	31	1	24	14
Third instar	H.L. ...	169 ± 5	130 ± 4			
	H.B. ...	100 ± 4	89 ± 3			
	O.R.B.	76 ± 3	67 ± 2			
	H.R. ...	1·69 ± 0·07	1·46 ± 0·05			
	No. ...	100	31			

H.L., H.B., O.R.B., H.R. and No. refer respectively to head length, head breadth, oral ring breadth, head ratio and number of larvae measured. * and ** indicate second and first+second instar data given in text.

coefficients. If this be correct, it would be anticipated that in overcrowded or nutritionally poor habitats the larvae would be small and the head size smaller than usual. So far, no evidence for this has been found in nature. On one occasion samples of larvae from two different breeding places were found to be very similar in appearance, but to differ in their head sizes. This difference was attributed to nutritional factors, but on rearing the larvae they were found to belong to two distinct species—*C. heliophilus* and *C. cubitalis.* A small but statistically significant difference has been found between laboratory reared and wild caught *C. nubeculosus* larvae (see p. 434).

Pigmentation.

Although there is considerable variation in the detailed distribution of the yellowish brown pigment found in *Culicoides* larvae, it is possible to arrange the species in a continuous series beginning with the most heavily pigmented and proceeding to those in which pigmentation is faint or absent. In *C. nubeculosus* and its allies, *C. stigma* and *C. riethi*, there is a superficial layer of pigment covering the thorax and most of the abdomen. In *C. salinarius*, *C. circumscriptus* and *C. odibilis* the abdominal portion of this layer is either absent or reduced to narrow intersegmental bars and in addition paired lateral pigmented bodies can be seen within the last two thoracic segments ; in the early instars these are compact and rounded in the mesothorax and longitudinally elongated in the metathorax. As pupation approaches, the mesothoracic bodies elongate and both they and the metathoracic bodies become concave outwards as they are pushed in by the developing imaginal buds. Transverse section of a *C. odibilis* larva (Pl. XVIII) shows that, in this species at least, the pigmented bodies are, in fact, associated with the dorsal side of the imaginal buds of the wings and halteres.

In the next group the covering of the mesothorax and metathorax is reduced and only the prothorax retains its complete superficial pigment layer. This arrangement is seen in *C. vexans*, *C. simulator* and *C. lupicaris*. When the complete covering is present in a segment it tends to be denser at the anterior border and to form a narrow transverse bar. In all the succeeding groups the prothorax is without a complete covering which, at the most, is represented by an anterior transverse bar and/or a broader transverse band. Thus *C. fascipennis*, *C. pictipennis* and *C. albicans* have both a transverse bar and a band in the prothorax whilst *C. pallidicornis* and *C. truncorum* have only a bar and *C. maritimus*, *C. cubitalis* and *C. heliophilus* only a band.

In the next group the prothoracic band is incomplete, consisting of paired lateral longitudinal bars and an irregular patch in the anterior median portion. In *C. delta*, *C. grisescens* and *C. halophilus* this patch is large, becoming smaller in *C. pulicaris*, *C. punctatus* and *C. cunctans* and finally in *C. impunctatus* it is either absent or poorly developed.

In the *C. obsoletus* group the antero-central prothoracic patch is either small or absent and the lateral longitudinal bars being shorter and broader than in the preceding group, closely resemble the paired mesothoracic bodies. These thoracic markings are heavily pigmented in *C. obsoletus* and *C. chiopterus* but are only faintly marked in *C. pseudochiopterus*. Lastly, there are three other Ceratopogonid genera (*Stilobezzia*, *Serromyia* and *Ceratopogon* (*Ceratopogon*)), which have *Culicoides*-like larvae. In these the paired lateral mesothoracic and metathoracic bodies, being devoid of pigment, appear grey and translucent.

KEY TO FOURTH-INSTAR LARVAE.

The following key to fourth-instar larvae of *Culicoides* and some other Ceratopogonid genera with vermiform larvae is based upon characters readily observed with low-powered oculars and objectives (×5 ocular and two-thirds and one-sixth objectives). It is best used with living or freshly preserved larvae, as some of the finer details are obscured or bleached in larvae which have been preserved for a long time. By a combination of pigment pattern, head colour and size it is usually possible to determine the larvae of most species, but there are certain cases where separation is, at present, very difficult—*C. salinarius* & *C. circumscriptus* ; *C. delta* & *C. pulicaris* ; *C. cunctans* & *C. punctatus* ; and *C. pallidicornis* & *C. truncorum*. Examination of the epipharynx enables the last two pairs to be separated.

Although these species are included in the key the epipharynges of *C. simulator*, *C. grisescens* and *C. delta* and the thoracic pigmentation of *C. scoticus*, have not been examined.

The head ratio (H.R.) and the head length will be given as a mean and a range, which includes two-thirds of the population. Throughout the key the term " bar " refers to a narrow linear strip of pigment and " band " to a broad area of pigment.

1. Long perianal bristles present..2
No obvious perianal bristles..3

2. Larvae very active, H.R. 1·5–1·8, front of head angular (Plate XVIII)............
Ceratopogon (*Isohelea*)
Larvae sluggish or active, H.R. >2·0, front of head rounded (Plate XVIII)......
Palpomyia, *Bezzia* etc.

3. Thoracic fat body grey and unpigmented..4
Thoracic fat body pigmented yellow brown..............................*Culicoides* 7

4. Head large, longer than 220 μ.......................................5
Head small, shorter than 180 μ.......................................6

5. Head amber-coloured (Plate XVIII), antennae inconspicuous.......................
Ceratopogon (*Ceratopogon*)
Head dark brown (Plate XVIII), antennae prominent......*Stilobezzia ochracea*
Stilobezzia gracilis

6. Larva swims in usual Ceratopogonid manner, H.R. 1·33 (1·30–1·36) (Plate XIV), about 20 teeth in dorsal comb of epipharynx ; teeth on lateral arm membranous ....*C. pseudochiopterus*
Larva never swims in usual Ceratopogonid manner, H.R. 1·48 (1·39–1·57) (Plate XVIII), about 14 teeth in dorsal comb ; teeth on lateral arm form narrow sclerotised plate..............................*Serromyia femorata*

7. Pharyngeal skeleton massive, epipharynx with heavy median block ; surface pigmentation covers dorsal surface of abdomen as well as thorax, paired lateral bodies either absent or difficult to see (Plate XIV)..........................
Culicoides nubeculosus Group 8
Pharyngeal skeleton lightly sclerotised, median block modified to form plate-like fourth comb ; pigmentation restricted to thorax, paired lateral mesothoracic and metathoracic bodies easily seen (Plate XIV)........................10

8. Head larger, about 330 μ long (305–369)..............................*nubeculosus*
Head smaller, about 270 μ long (260–282)..............................9

9. Free margin of hypostomium (labium) strongly sclerotised ; dorsal comb 42 μ wide, median block 52 μ wide ; found in brackish water..................*riethi*
Free margin of hypostomium not differentiated from the rest of the head capsule ; dorsal comb 34 μ wide, median block 42 μ wide ; found in fresh water......
stigma

10. Head < 180 μ long, prothoracic paired lateral bodies similar to mesothoracic (Plate XIV) ; epipharynx with two or three combs only..........................
C. obsoletus Group 11
Head > 180 μ, or if shorter, then thoracic markings otherwise ; epipharynx with four combs..............................14

11. Head yellow, very small and nearly square (115 μ by 99 μ), H.R. 1·16 (1·11–1·21) ; fourth (ventral) comb with about five teeth, second and third combs absent ....*chiopterus*
Head amber or yellow, > 150 μ, H.R. 1·27–1·43 ; fourth comb with 12 teeth or three combs present..............................12

12. Pigmentation of all thoracic segments faint (Plate XIV) ; second and third combs absent, fourth with 12 teeth..............................*pseudochiopterus*
Pigmentation in prothorax and mesothorax distinct (Plate XIV) ; second or third comb present..............................13

13. Second comb absent, fourth with six teeth..............................*obsoletus*
Fourth comb absent, dorsal comb with median tooth..............................*scoticus*

14. Conspicuous paired latero-median pigmented bodies in hind portion of prothorax ; head pale yellow, 270 μ long (261–275), narrow, H.R. 1·75 (1·70–1·80) (Plate XVI) ....*albicans*
Markings and head otherwise..............................15

15. Prothorax covered with diffuse pigmented network, head usually yellow......16
Postero-median portion of prothorax unpigmented, head often amber.........20

16. Head larger (> 300 μ), amber-coloured (Plate XV), dorsal comb with 30 teeth........ *lupicaris*
Head never more than 280 μ long and usually shorter, lighter ; dorsal comb with less than 25 teeth........17

17. Postero-median portion of mesothorax unpigmented, metathoracic bodies faintly pigmented (Plate XV)........18
Mesothorax more or less completely pigmented, metathorax diffusely but distinctly pigmented (Plate XV)........19

18. Head larger, 267 μ (262–272)........*vexans*
Head smaller, 205 μ long........ *simulator*

19. Head larger, about 230 μ long (222–241)........*circumscriptus*, *salinarius*
Head smaller, 190 μ long (186–194)........ *odibilis*

20. Prothorax with distinct transverse bar on anterior margin and with or without a transverse band (Plate XVI)........21
Prothorax never with anterior transverse bar but sometimes with a broad transverse band (Plate XVII)........24

21. Head larger, about 245 μ (239–252) long........22
Head smaller, about 200 μ (194–210)........23

22. Head pale yellow, narrower H.R. 1·67 (1·58–1·76)........*pictipennis*
Head amber, broader H.R. 1·51 (1·45–1·57)........ *fascipennis*

23. Dorsal comb with median tooth (fig. 17)........ *truncorum*
Dorsal comb without median tooth........*pallidicornis*

24. Prothorax with an irregular pigmented patch on its anterior margin, head amber-coloured (Plate XVII)........25
Prothorax either unmarked or with a transverse band, head yellow (Plate XVII)........30

25. Head muddy brown in colour, central prothoracic patch poorly developed or absent (Plate XVII)........ *impunctatus*
Head amber-coloured, usually with a well developed patch in centre of anterior margin of prothorax........26

26. Larvae found in brackish water ; always with a large irregular antero-central prothoracic patch (Plate XVII), dorsal comb with median tooth (fig. 30)...... *halophilus*
Larvae found in fresh water ; development of prothoracic patch variable ; dorsal comb with or without median tooth........27

27. Head length 240 μ or less........28
Head length 245 μ or more........29

28. Dorsal comb with median tooth (fig. 26)........ *cunctans*
Dorsal comb without median tooth........*punctatus*

29. Prothoracic patch narrows anteriorly........*grisescens*
Lateral margins of prothoracic patch either parallel or converging posteriorly *pulicaris*, *delta*

30. Conspicuous transverse bands in all thoracic segments, head longer, 225 μ (218–232) (Plate XVI)... *maritimus*
No transverse band in either mesothorax or metathorax, head shorter, less than 200 μ (162–197) (Plate XVII)...31

31. Prothoracic transverse band conspicuous, head larger, 191 μ (185–197) ; living larva floats on water ; dorsal comb 37 μ wide.......................... *heliophilus*
Prothoracic transverse band varies from faint to distinct, head smaller, 166 μ (162–170) ; larva sinks in water ; dorsal comb less than 25 μ wide... *cubitalis*

General Features of the Larvae.

A detailed account of the larva of *C. nubeculosus* has been given by Lawson (1951). Except in the pharyngeal skeleton, the larvae of most species of *Culicoides* and of the other genera described here differ from that of *C. nubeculosus* only in minor points.

The *Head Capsule* in most species closely resembles that of *C. nubeculosus* in structure, being composed of only three sclerites : a dorsal sclerite, the fronto-clypeus, separated by the frontal or ecdysial suture from the sclerite of complex origin making up the lateral and ventral walls, which is itself separated by the post-occipital suture from the third sclerite, the post-occipital ridge or collar. In *Ceratopogon* (*Ceratopogon*) and *Ceratopogon* (*Isohelea*) (fig. 7), however, there is a well-developed, sclerotised and pigmented suture extending forwards in the mid-ventral line from the post-occipital ridge for about one-third of the length of the head. A similarly placed suture is present in *Stilobezzia ochracea*, *C. albicans*, *C. lupicaris*, *C. pulicaris* (or *C. delta*), *C. punctatus*, *C. halophilus* and *C. fascipennis* (figs. 5 and 8), but in these the suture is unsclerotised and unpigmented and is rather a line of weakening than a line of strengthening. The existence of this suture in these species helps considerably in establishing the homologies of the lateral and ventral walls of the cranium.

There is some slight variation in the degree of sclerotisation and pigmentation of the hypostomium, but this occurs to a marked extent only in *C. riethi* (fig. 3).

In all species of *Culicoides* the antennae are small and unobtrusive, but in *Stilobezzia* (fig. 8) and *Isohelea* (fig. 6) they are quite prominent.

The *Mandibles* have been figured in some previous descriptions in the belief that their variation is of specific value. This belief is probably correct, but, in the entire larva, they are often retracted and difficult to see, and, when they are dissected out, a slight alteration in their position makes a considerable change in their appearance, so that comparable figures are difficult to obtain. For this reason descriptions of the mandibles are not given here.

The *Setae* of the head and body are almost always simple and their arrangement is constant throughout the genus and also probably throughout the family, so far as the setae of the head are concerned. The details of their form and occurrence in *C. nubeculosus* and a comparison with those found in *Forcipomyia* by Saunders (1924) have been given by Lawson (1951). Interspecific variation consists almost entirely in relatively small differences in size, or, in the case of some minor setae, of presence or absence. The minor setae, however, especially of the body, are occasionally of such size that they require to be searched for with a 1/12th oil-immersion objective and even then are readily overlooked. In most species the longest setae of the head are about as long as one-third to a half the width of the head ; only in a few species are they longer (*C. odibilis*, *C. heliophilus*) or much shorter (*C. nubeculosus*, *C. riethi*, *C. pseudochiopterus*).

Occasionally some of the body setae are multiple, *i.e.*, a number of setae arise from one base ; but this feature is not constant—it has been found in some specimens of *C. odibilis* and of *C. obsoletus* and not in others. In a single specimen of *C. pseudochiopterus* the pair of setae "*s*", just in front of the eye and outside the frontal suture, have also been found to be multiple ; this is the only case in *Culicoides* in which setae of the head were multiple. In *Ceratopogon* and *Isohelea* (fig. 6), however, the seta " *s* " is always multiple and in the latter, the setae " *x* ", on the inner margin of the antennae, are also multiple. In *Stilobezzia ochracea* (fig. 8) the setae " *o* ", near the lateral margins of the hypostomium, are multiple.

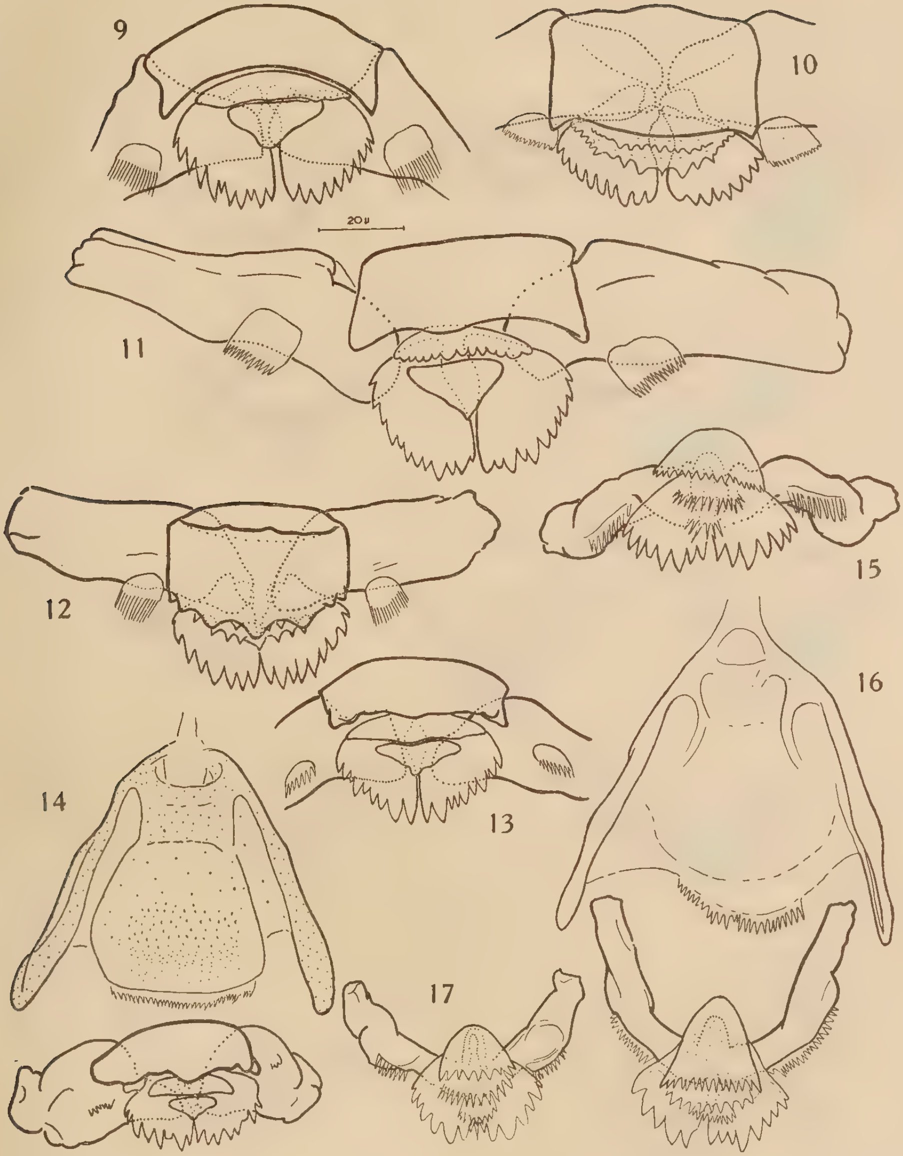
In the *C. nubeculosus* group the labrum bears two pairs of large setiform sensillae on its anterior face (fig. 4) ; in all the rest of the genus these are represented by two pairs of normal small setae.

The *Pharyngeal Skeleton* enables each species of *Culicoides* to be placed in one of two distinct groups, the *C. nubeculosus* group and a group consisting of the rest of the genus. The details of this structure in *C. nubeculosus* and a discussion of its homologies have been given by Lawson (*l. c.*). Throughout the genus the structure consists essentially of a ventral hypopharynx (figs. 14, 16 and 39), trough-like in its posterior region, and, working in and against this trough, a complex, dorsal epipharynx slung from two lateral, sclerotised arms. As in *Forcipomyia* and *Tetraphora* (= *Dasyhelea*), all these components are heavily sclerotised and pigmented in the *C. nubeculosus* group. The epipharynx (figs. 9–14) in this group consists of a massive, solid, median block bearing on the posterior face a pair of roughly triangular sclerites, the posterior edges of which are toothed. Ventral to this pair are two smaller, median sclerites. The lateral arms of the epipharynx each bear a single sclerite on which the powerful retractor muscles are inserted. From the massiveness of its components the skeleton of this type appears to be a grinding and crushing apparatus. Within the group the epipharynx presents a series in which the two small median sclerites and the postero-ventral edge of the median block, at first smooth and plain, develop rounded projections and finally, definite teeth. The group is thus linked with the type found in the rest of the genus.

In the second type the degree of sclerotisation and pigmentation is very much less ; the trough of the hypopharynx (fig. 16) in particular is almost completely membranous, and its posterior edge is prolonged into fine membranous teeth. The epipharynx consists of a pair of dorsal toothed sclerites, corresponding to those of the first type, and, in addition, ventral to these, of one to three plate-like sclerites, the posterior edges of which are also toothed. These will be referred to as " combs ", in the order " dorsal comb ", second, third and fourth combs, proceeding ventrally. The median block of the first type is here very much reduced, being represented by the fourth comb, the most ventral, which is usually a plate curved into the shape of half a cone. The small, median sclerites of the first type are here represented by the second and third combs. The small separate sclerites on the lateral arms in the first type are replaced in the second by a fringe of membranous teeth. The comparative lightness of this type of structure suggests that it is incapable in effect of carrying out the grinding and stamping movements which have been observed in *Tetraphora* and probably occur in the *C. nubeculosus* group. Instead the function of this apparatus is more likely to be that of sucking and sieving.

In the species of *Culicoides* having this type of skeleton only those of the *C. obsoletus* group have less than four combs. In *C. scoticus* (fig. 34) the absent comb is the fourth : in the rest of the *C. obsoletus* group it is the second or third comb or both which is missing.

The specific variation in the pharyngeal skeleton consists in differences in size, in the shape of the combs, and in their number, of course, and in the number and size of their teeth. The individual variation appeared to be slight. In 13 specimens of *C. cubitalis* there were small differences in the number of teeth on the combs, but the pattern was demonstrably the same. The size of the skeleton, as measured across the dorsal comb, was also reasonably constant : the average width was 22 μ, with a range of ± 2 μ. It appears therefore, that in the case of different species with a



PHARYNGES OF THE LARVAE

In each case the figures show the epipharynx from the ventral side. The often apparently considerable differences in the lateral arms are insignificant, being due, in most cases, to relatively small variations in the angle from which the drawing was made. Figures 14, 16 and 39 show a dorsal view of the hypopharynx in addition to the epipharynx.

Fig. 9. *C. nubeculosus*. Dorset. Common form.

Fig. 10. (?) *C. nubeculosus*. Dorset. Unusual form.

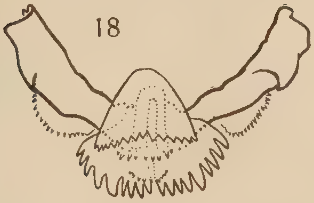
Fig. 11. *C. nubeculosus*. Inverness-shire.

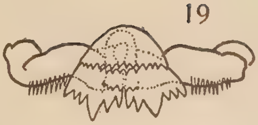
Fig. 12. *C. nubeculosus* group. Westphalia (B.M. No. 478, tube 8).

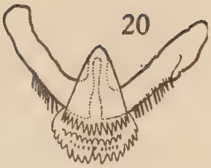
Fig. 13. *C. riethi*. Fig. 14. *C. stigma*. Fig. 15. *C. vexans*.

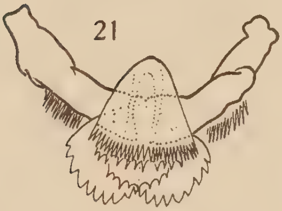
Fig. 16. *C. albicans*, epipharynx and dorsal view of hypopharynx.

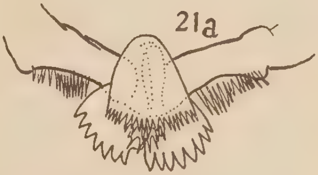
Fig. 17. *C. truncorum*.

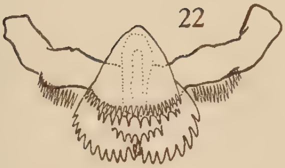


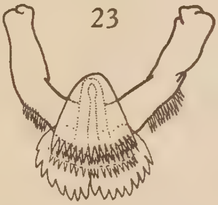


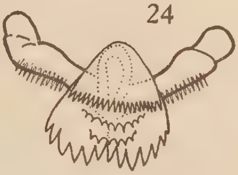


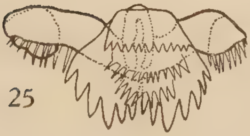


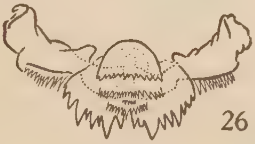


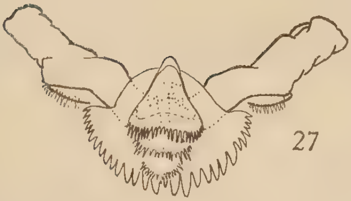


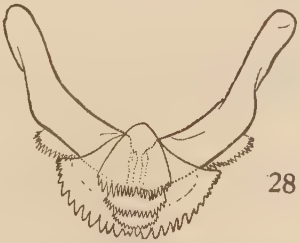












PHARYNGES OF THE LARVAE

FIG. 18. *C. fascipennis.*
FIG. 19. *C. pallidicornis.*
FIG. 20. *C. cubitalis.*
FIG. 21. *C. salinarius.*
FIG. 21a. *C. pictipennis.*
FIG. 22. *C. circumscriptus.*
FIG. 23. *C. odibilis.*
FIG. 24. *C. maritimus.*
FIG. 25, *C. heliophilus.*
FIG. 26. *C. cunctans.*
FIG. 27. *C. lupicaris.*
FIG. 28. *C. pulicaris.*

similar pattern in the pharyngeal skeleton, as in *C. cubitalis* (fig. 20) and *C. odibilis* (fig. 23), it is possible to distinguish them by the difference in the width of the dorsal comb.

The pharyngeal skeleton of *Stilobezzia*, *Ceratopogon* and *Isohelea* is, in each case, essentially similar to the lightly sclerotised type of *Culicoides*, but the pattern is appreciably different. It is interesting to note that the relation of these genera to *Culicoides* is through the *C. obsoletus* group, whereas *Forcipomyia* and *Tetraphora* are related through the *C. nubeculosus* group.

In order to make a satisfactory examination of the pharyngeal skeleton it was necessary, as has already been indicated, to dissect it out—a process which almost always involved the complete destruction of the head capsule. The preparation for this consisted in gently boiling the head in 10 per cent. potash for a few minutes, followed by further treatment for a few minutes with hot, pure lactic acid in which was dissolved a small quantity of Solway Green. This neutralised the alkali, completed the clearing and also stained the sclerotised structures a bright green, so that the smaller combs could be rather more easily seen. The head was then transferred to a drop of polyvinyl alcohol mounting medium on a slide, where the dissection was carried out and the epipharynx was detached from the hypopharynx. Further manipulation of the cover slip was necessary in order to manoeuvre the epipharynx into a position with its ventral side uppermost.

The figures of the epipharynges are all camera lucida drawings to the same scale, presenting the ventral side uppermost. Apparent variations in the angle of attachment of the lateral arms, some of which are shown cut short, are due to variations from the true upside-down position. Such variations have a negligible effect on the appearance of the epipharynx itself.

First Instar Pseudopod.—A prothoracic pseudopod is present in the first instar of *C. nubeculosus*, *C. scoticus* (fig. 42) and *C. obsoletus* (fig. 41), in the last of which it was first observed by Mr. A. H. Parker (private communication). In position and appearance this pseudopod closely resembles that found in the fourth instar of *Apelma* by Saunders (1925). It is not, however, a constant feature in first instar *Culicoides*, for it was absent in *C. halophilus*, the only other first instar examined.

Internal Anatomy.—A curious variation in the length of the oesophagus occurs in *C. albicans* and *C. impunctatus*, where the proventricular valve, the junction between the oesophagus and the mid-gut, is situated in the fourth and third abdominal segments respectively. In all other species examined it is situated in the metathorax.

C. albicans also shows another peculiarity in that ganglia of the ventral nerve cord tend to be spheroidal, whereas in the rest of the genus the ganglia are elongate ovoid.

DESCRIPTIONS OF LARVAE OF CULICOIDES.

Culicoides nubeculosus (Meigen) (Plate XIV).

The larvae and pupae grouped under this name are heterogeneous, those from Dorset being generally distinct from those taken in Inverness-shire. The two forms will be referred to as Forms *A* and *B* but there is as yet, no satisfactory method of separating the adults.

Form A—Fourth Instar.—Head 315 μ by 217 μ, H.R. 1·45, dirty brownish yellow with brown mandibles and oral ring (128 μ) and a dark brown to black collar. The massive dark brown pharynges (=pharyngeal skeleton) appear as a solid transverse bar in the centre. *Epipharynx* (fig. 9). The dorsal combs each bear about 10 sharp, irregular teeth, and the width across the pair is about 53 μ. Ventral sclerites not toothed, the first roughly triangular, with its base abutting closely against the edge of the next sclerite. Median block simple, without trace of teeth on its posterior edge, about 56 μ wide. One specimen of the 17 examined (fig. 10), which was otherwise not distinguished from the rest, was only slightly smaller, the width across both the dorsal combs and the median block being 48 μ. The ventral sclerites, however, were quite different being clearly but irregularly toothed, and thus obviously corresponded to the second and third "combs" found in the rest of the genus. *Thoracic Markings.*—The whole dorsal surface, including prothoracic ring covered with a superficial layer of small, irregular aggregations of yellowish brown pigment.

Third Instar.—Head smaller and paler than that of fourth, 209 μ by 137 μ and 84 μ wide at oral ring, H.R. 1·52. Thoracic pigment more granular than that of fourth instar. Individual granules smaller than in Form *B* with pale centre very small or lacking.

Second Instar.—Very similar to third. Head 126 μ±4 by 88 μ±3, and 57 μ±2 wide at oral ring, H.R. 1·49±0·02 (15 larvae).

First Instar.—Very similar to second. Head 79 μ±4, 62 μ±5, and 39 μ±2 wide at oral ring, H.R. 1·27±0·13 (16 larvae).

Source of Material.—(i) Numerous adults bred from larvae brought by Mr. J. A. Downes from a farmyard at Chideock, Dorset, have been used to start a laboratory culture. A sample of 26 laboratory reared fourth-instar larvae had the following mean head measurements and 95 per cent. fiducial intervals :—324 μ±4 ; 218 μ±2 and 131 μ±2 compared with 315 μ±5 ; 217 μ±5 and 128 μ±3 for wild caught larvae. The difference in the head lengths is statistically significant ($P<0·01$). (ii) Ten specimens, Dreghorn, Ayrshire, 1919, F. W. Edwards, British Museum, Natural History (Number 146). Means and standard deviations of head measurements 359 μ±10 ; 222 μ±8 and 137 μ±5 ; H.R. 1·57±0·05, the pharynges of one of these proved to be normal Form *A*.

Breeding Places.—In muddy hoofprints near farmyards, often associated with larvae of *C. circumscriptus*, *C. stigma* and *C. odibilis*.

Form B—Fourth Instar.—Head brownish yellow, rather darker and larger, 347 μ by 224 μ, than that of Form *A*, H.R. 1·55. Mandibles and oral ring (141 μ) brown and the collar almost black. *Epipharynx* (fig. 11) having dorsal comb almost semicircular in shape with 11 or 12 sharp, irregular teeth on each side of the mid-line : width across the comb about 51 μ. The small triangular median sclerite on ventral side of dorsal comb similar to that of Form *A* ; but the next sclerite has its posterior edge divided into about 14 rounded, irregular teeth. The median block (width 60μ) has three rounded projections on the postero-ventral edge, one at each side and one in the mid-line. *Thoracic Markings* same as in Form *A* but pigment more coarsely particulate.

Third Instar very similar to fourth but head 217 μ by 134 μ and 83 μ wide at oral ring ; H.R. 1·59. The large pigment clumps consist of a thin layer of pigment arranged around a large clear centre.

Breeding Places and Source of Material.—In a patch of wet mud, bearing a growth of blue-green alga and, fed by drainage from a heap of stable refuse, in a farmyard at Auchteraw, Fort Augustus, Inverness-shire. 3♂♂ and 2♀♀ have been reared from larvae of this type.

Unknown Species related to C. nubeculosus (fig. 12).

Among larvae of *C. salinarius* in the collection of the British Museum (Natural History) (see p. 440), there were two which, from their appearance and the size of the pharynges, were clearly related to *C. nubeculosus*. In one of these, the epipharynx embodied a further stage in the development of the combs. In the dorsal comb (width 44 μ) there were 8–9 teeth on each side. In the second and third combs there were 8 and 7 teeth respectively. The median block had its postero-ventral margin produced into 7 rounded projections separated by wide shallow indentations, thus resembling teeth.

Culicoides riethi Kieffer.

Fourth Instar.—Head 271 μ by 178 μ, H.R. 1·52, brownish yellow with massive dark brown pharynges, black collar, light brown mandibles and oral ring (117 μ). Very similar to that of *C. stigma* but with a unique degree of sclerotisation along the free margin of the hypostomium (fig. 3). *Epipharynx* (fig. 13) having two parts of dorsal comb (width 42 μ) completely separate, with their posterior edges sloping forwards laterally; each with 9 or 10 teeth, the first and second from mid-line being much enlarged. Ventrally of these there are two small median sclerites with slight, irregular, tooth-like projections. Median block (width 52 μ) with about 6 more or less regularly rounded projections on postero-ventral edge. *Thoracic Markings.* A superficial layer of pigment covers the dorsal surface but its detailed structure could not be discerned in the specimens available.

Third Instar unknown.

Source of Material.—Westphalia, salt water, Thienemann, 1922, 478–7, British Museum (Natural History). The associated adults were too faded to identify but the terminalia of 6♂♂ agreed with Edwards' (1939) description of *C. riethi*.

Culicoides stigma (Meigen) (Plate XIV).

Fourth Instar.—Head 268 μ by 166 μ, H.R. 1·62, brownish yellow with massive pharynges, black collar, brown mandibles and oral ring (101 μ). Very similar to that of *C. riethi* but smaller and less brown than either form of *C. nubeculosus*. *Epipharynx* (fig. 14) having each side of the dorsal comb (width 34 μ) with about 8 sharp, irregular teeth. The small ventral, median sclerites toothless and the first (=second comb) almost transparent. Median sclerotised block (width 42 μ) with smooth indentations and projections irregularly placed along its postero-ventral edge, resembling broad, rounded teeth. *Thoracic Markings.*—Dorsal surface covered with a superficial layer of reddish brown pigment, composed of irregular clumps, larger than those of *C. nubeculosus* Form *A* and lacking the distinct pale centre of Form *B*. On the abdomen this layer is less well developed than in other members of the *C. nubeculosus* group.

Third Instar.—Very similar to fourth. Head 180 μ by 113 μ and 72 μ wide at oral ring, H.R. 1·63.

Adults Reared 14♂♂, 11♀♀ *C. stigma* and 1♀ *C. odibilis* (accidental introduction).

Sources of Material and Breeding Places.—Drumchapel, Glasgow, Lanarkshire, Strathglass and Glen Urquhart, Inverness-shire. It breeds often with *C. nubeculosus*, *C. circumscriptus*, *C. odibilis* in mud which may dry up completely in summer.

Notes.—Among the larvae described here only those of *C. stigma* have been parasitised by larvae of Gordiacea. We are indebted to Dr. G. Lapage for this identification.

Culicoides vexans (Staeger) (Plate XV).

Fourth Instar.—Head 267 μ by 186 μ, H.R. 1·43, bright yellow with brown mandibles, oral ring (136 μ) and collar. *Epipharynx* (fig. 15). All *Culicoides* outside the *C. nubeculosus* group have only lightly sclerotised pharynges without a heavy median block; instead there are the dorsal and three superimposed ventral combs, the most ventral of which probably represents the median block. Dorsal comb (width 43 μ) with 7–8 large, sharp teeth on each side; second with about 7 long, fine teeth, rather indistinct; third with 12–14 long, fine teeth, rather irregularly disposed and difficult to see; the fourth, ventral, with 19–22 sharp, triangular-shaped teeth, is rounded anteriorly. *Thoracic Markings.*—Prothorax covered with a layer of bright yellowish brown pigment. Paired lateral mesothoracic bodies expanded anteriorly to join and form a broad transverse band, which leaves the postero-median portion unpigmented. Paired lateral metathoracic bodies only faintly pigmented and not expanded.

Third Instar unknown.

Adults Reared 16♂♂, 15♀♀ *C. vexans* and 1♀ *C. pulicaris* (accidental introduction).

Source of Material and Breeding Place.—Abbotsbury, Dorset, in mud-lined shallow pools in a waterlogged hayfield, which undoubtedly dried up in summer; it seems likely that this period is passed in the egg stage since Jobling (1929) found that eggs, laid in June, did not hatch until October. Fifty-four larvae, obtained on 5th April, all nearing pupation, completed emergence in the laboratory by 25th April. This agrees with Edwards (1939) who observed that the adults are abundant in late April and May.

Culicoides albicans (Winnertz) (Plate XVI).

Fourth Instar.—*Head* 268 μ by 155 μ, H.R. 1·75, with an unsclerotised ventral posterior suture. Pale straw coloured; mandibles pale amber, oral ring pale brown (117 μ) and collar dark brown. *Epipharynx* (fig. 16) having each half of the dorsal comb (width 40 μ) with 5–9 rather large irregular teeth; second with about 10 rather long, sharp teeth; third with about 10 broadly triangular, sharp, well-separated teeth; the fourth, ventral, with about 15 sharp, triangular teeth. *Thoracic Markings.*—Prothorax with narrow paired lateral bars joined anteriorly by a narrow transverse bar, which is continued on the ventral surface. Posteriorly a ring of pigment, encircling the oesophagus, is expanded into two lateral clumps, which are continued anteriorly as tapering prolongations. This arrangement is characteristic and has not been observed in any other *Culicoides* larvae. In addition there is a diffuse transverse band. The mesothorax and metathorax contain the usual lateral markings.

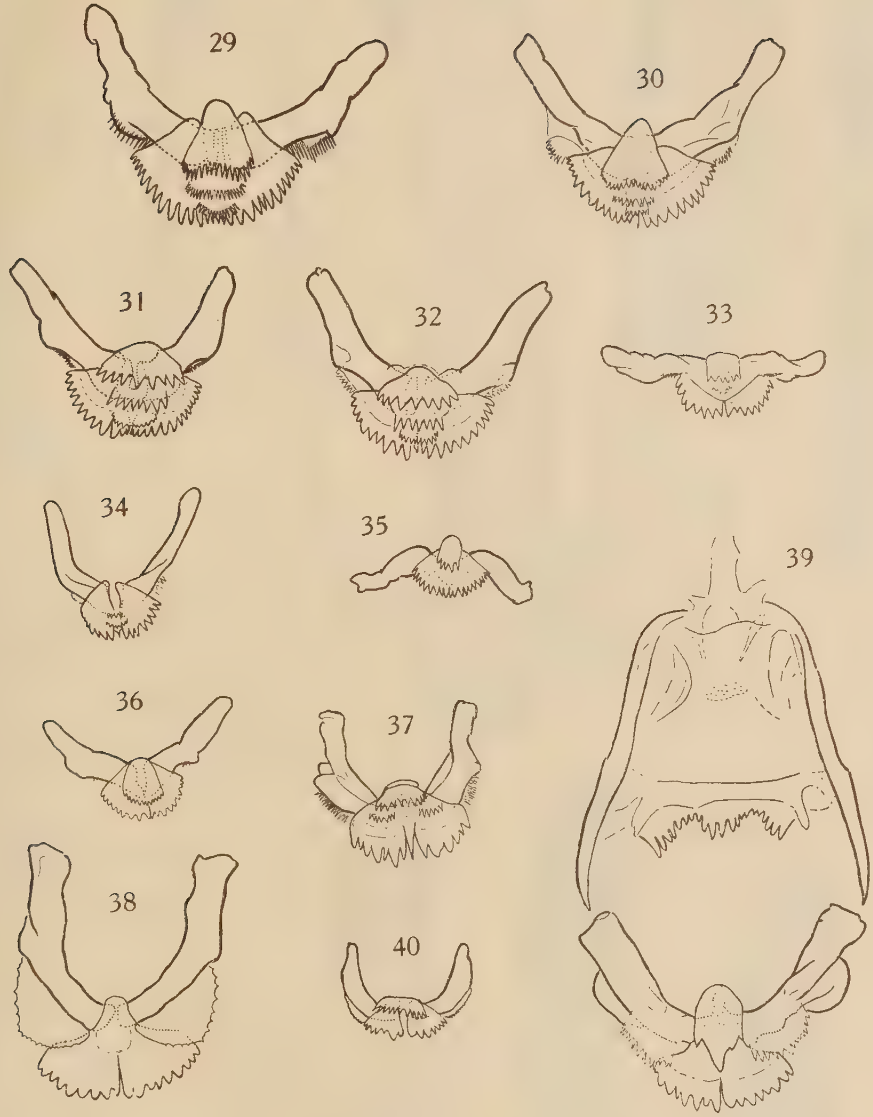
Third Instar differs from 4th in the poorer development in the prothorax of both the anterior bar and the transverse band. Head 179 μ by 103 μ and 80 μ wide at oral ring, H.R. 1·75.

Adults Reared 1949–51; 10♂♂, 2♀♀ *C. albicans* and 1♀ of uncertain specific status.

Sources of Material and Breeding Places.—Loch Lomond and Milngavie, Dumbartonshire; Glasscarnock, Inverness-shire; Glen Glova, Angus; Trossachs, Perthshire; and Strathgryfe, Renfrewshire, where it breeds, but never abundantly, in wet areas of bogland in association with *C. impunctatus*, *C. heliophilus* and *Ceratopogon* (*Isohelea*).

Culicoides truncorum Edwards (Plate XVI).

Fourth Instar.—*Head* 203 μ by 134 μ and 98 μ wide at oral ring; light amber with light brown mandibles, collar and oral ring, H.R. 1·52. *Epipharynx* (fig. 17) having dorsal comb (width 33 μ) with a single long, thin, sharp, median tooth and on each side 7–8 teeth, of which the second and third from the mid-line are rounded and larger than the rest; second comb with about 9 teeth; third with about 12 teeth; the fourth with about 9 teeth. *Thoracic Markings.*—Prothorax with a narrow transverse bar of pigment anteriorly and antero-laterally small markings shaped like inverted exclamation marks (¡). Both the mesothorax and metathorax have in addition to the usual paired lateral bodies, anterior transverse bars which arise from small forwardly placed lateral patches and spread inwards whereas the prothoracic bar originates in the centre and spreads laterally. In general appearance *C. truncorum* is indistinguishable from *C. pallidicornis* although the head of the latter is darker.



PHARYNGES OF THE LARVAE

FIG. 29. *C. punctatus.*

FIG. 30. *C. halophilus.*

FIG. 31. *C. impunctatus.* Scotland.

FIG. 32. *C. impunctatus.* Liverpool. Hill's (1947) specimen.

FIG. 33. *C. obsoletus.*

FIG. 34. *C. scoticus.*

FIG. 35. *C. chiopterus.*

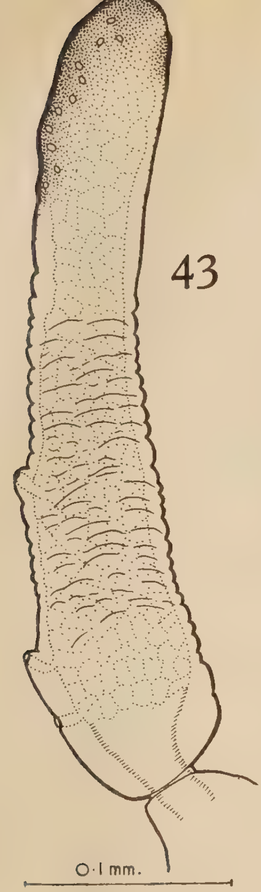
FIG. 36. *C. pseudochiopterus.*

FIG. 37. *Ceratopogon* (*Ceratopogon*).

FIG. 38. *Ceratopogon* (*Isohelea*).

FIG. 39. *Stilobezzia ochracea,* epipharynx and dorsal view of hypopharynx.

FIG. 40. *Serromyia femorata.*



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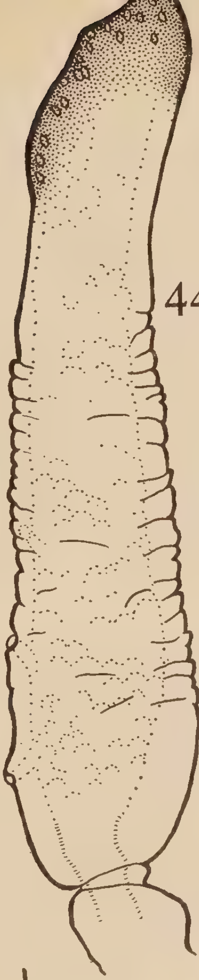

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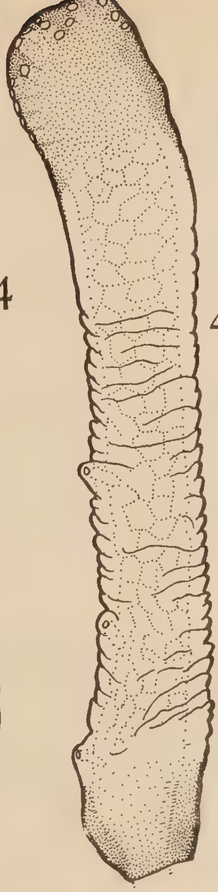

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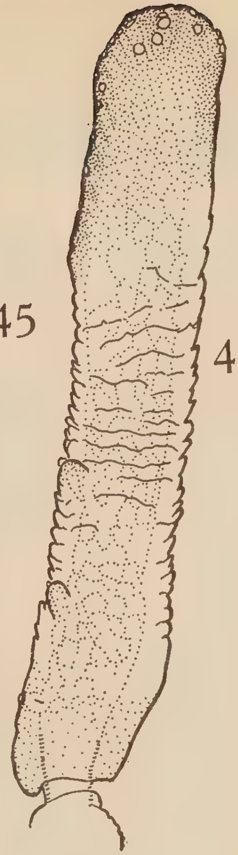

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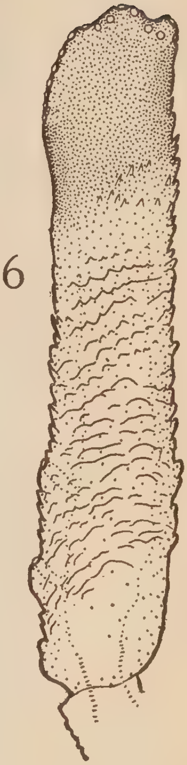

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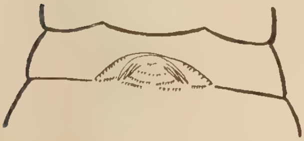

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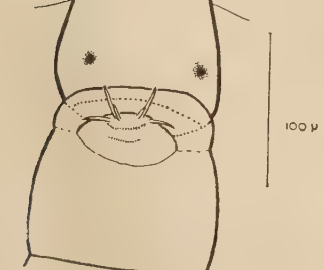

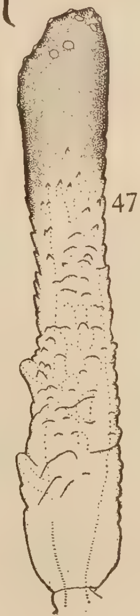

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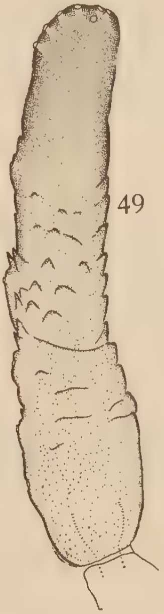

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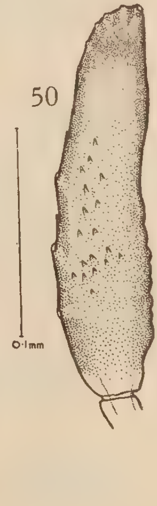

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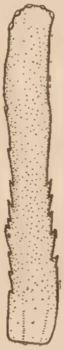


Fig. 41. (?) *C. obsoletus*, prothoracic pseudopod of 1st instar.

Fig. 42. *C. scoticus*, prothoracic pseudopod of 1st instar.

PUPAE. PROTHORACIC RESPIRATORY HORN

In each case the figure shows a lateral (outer) view of the right prothoracic horn.

Fig. 43. *C. nubeculosus*. Dorset. Fig. 44. *C. nubeculosus*. Inverness-shire.

Fig. 45. *C. nubeculosus*. Ayrshire. Fig. 46. *C. riethi*. Fig. 47. *C. stigma*.

Fig. 48. *C. parroti*. Fig. 49. *C. vexans*. Fig. 50. *C. albicans*. Fig. 51. *C. truncorum*.

Third Instar very like fourth, except that all markings are rudimentary, especially the transverse bars, which are often absent. Head 144 μ by 93 μ and 71 μ wide at oral ring, H.R. 1·55.

Second Instar markings very reduced ; no pigmentation in prothorax and no transverse bars in either mesothorax or metathorax. Head 101 μ±4 by 66 μ±4 and 51 μ±3 at oral ring. H.R. 1·55±0·09 (49 larvae).

First Instar very similar to second but the head is 72 μ±3 by 48 μ±2 and 37 μ±2 wide at oral ring. H.R. 1·52±0·11 (30 larvae).

Adults Reared 1948–51 ; 14♂♂, 36♀♀. The females are difficult to identify with certainty on account of the faintness of the pale areas around the wing tip, but the male terminalia are specific and all agreed with Edwards' (1939) figure.

Sources of Material and Breeding Places.—Luss, Loch Lomond and Trossachs, Perthshire. This species has been found, often abundantly, in bogland sites dominated by *Sphagnum* spp. in which it is associated with *C. impunctatus* and *Ceratopogon* (*Isohelea*). This may prove to be a useful way of separating *C. truncorum* from *C. pallidicornis*, which prefers marshland breeding sites and has not been found in *Sphagnum* spp.

Notes.—The vertical distribution of *C. truncorum* larvae is given in Table II. It will be noticed that the first and second instars have very similar distributions with 75 per cent. occurring in the first inch, whereas the third and fourth instars have 34–39 per cent. in each of the first two inches. The X^2 test indicates that this difference is unlikely to be the result of experimental error ($P<0·001$). The distributions of instars 1 and 2 are statistically inseparable ($P=0·6$) and the same is true for instars 3 and 4. There are three possible explanations of this observation. Firstly instars 3+4 and 1+2 may represent different species. This is unlikely since the head measurements closely approximate to Dyar's Law (fig. 1) and second instars have been observed moulting to third. Secondly the different distributions of the two groups may indicate a different length of life in the soil ; that is, the species may have two generations a year in which emergence is incomplete. Since these observations were made in the late autumn of 1947 it would mean that instars 1+2 would be the progeny of an autumn generation and instars 3+4 the progeny of a spring generation. Lastly the species could take two years over a generation. In this case instars 1+2 would have originated from the 1947 adults and instars 3+4 from 1946 adults. There is no evidence to decide which of these is the more accurate interpretation.

Culicoides fascipennis (Staeger) (Plate XVI).

Fourth Instar.—*Head* 247 μ by 164 μ, H.R. 1·51, amber with an unsclerotised ventral suture ; collar, mandibles and oral ring (115 μ) dark brown. *Epipharynx* (fig. 18) having dorsal comb (width 38 μ) nearly semicircular in outline with 9–10 teeth on each side, of which the fourth or fifth from the mid-line are obviously the largest ; second indistinct and semicircular with about nine triangular teeth ; third with an irregular row of about nine irregularly placed teeth ; the fourth with about 15 sharp, triangular shaped teeth. The anterior region of the sclerite is membranous and indistinct. *Thoracic Markings.*—Prothorax with a pair of lateral bars joined anteriorly by a narrow transverse bar and across the dorsum by a broader band which may be faint or even absent. Mesothoracic lateral bodies meet anteriorly in the mid-dorsal line but the metathoracic bodies although expanded anteriorly do not fuse. The prothoracic and mesothoracic pigment is much darker than that in the metathorax.

Third Instar similar to fourth except that the markings are less developed ; in particular, the prothoracic transverse band is absent. Head 156 μ by 96 μ and 76 μ wide at oral ring H.R. 1·62 (two larvae).

Adults Reared 13♂♂, 16♀♀.

Sources of Material and Breeding Places.—Loch Achray, Perthshire ; Milngavie, Dumbartonshire ; Glasscarnock and Strathglass, Inverness-shire and Glen Clova, Angus, where the larvae were found in mud among semi-aquatic plants (*Carex* spp. and *Scirpus palustris*) near an open body of water, so that at some periods of the year the breeding places are probably under water.

Culicoides pallidicornis Kieffer (Plate XVI).

Fourth Instar.—Head slightly smaller and darker than *C. truncorum* ; 199 μ by 130 μ and 93 μ wide at oral ring, H.R. 1·53 ; mandibles, collar and oral ring light brown. *Epipharynx* (fig. 19) having dorsal comb (width 31 μ) with about six teeth in each half, the third from the middle line on each side being very large ; second comb with about eight short teeth ; third with six teeth and the fourth with about 15 short, sharp teeth. *Thoracic Markings* identical with those of *C. truncorum* (see p. 436).

Third Instar similar to fourth but head 139 μ by 92 μ and 67 μ wide at oral ring, H.R. 1·51.

Adults Reared 1948–51 ; 23♂♂, 34♀♀ and 1♂ *C. odibilis* (accidental introduction).

Sources of Material and Breeding Places.—*C. pallidicornis* or *C. truncorum* larvae have been found in many breeding places but only those from which *C. pallidicornis* has been reared will be considered. Drumchapel, Lanarkshire ; Trossachs, Perthshire ; Bridge of Weir, Renfrewshire and Balmaha and Pass of Balmaha, Stirlingshire, where they were found in association with *C. cubitalis* in marshy ground bearing *Ranunculus* spp. and *Cardamine* spp. and mosses but no bog-moss (*Sphagnum* spp.).

Culicoides cubitalis Edwards (Plate XVII).

Fourth Instar.—Head 166 μ by 104 μ, H.R. 1·60 ; very pale straw-coloured ; mandibles straw-coloured, collar and oral ring (74 μ) light brown. *Epipharynx* (fig. 20) of thirteen specimens from nine different sites were examined in order to arrive at some idea of the individual variation of the pharynges. There was some small variation in the number of teeth on the combs, but the pattern was clearly the same and width across the dorsal comb was constant within ±2 μ ; the larva with the smallest pharynges was associated with a larva having pharynges of average size, and that with the largest pharynges was taken from a depth of 3–4 metres in Loch Lomond by Dr. A. C. J. Weerekoon. Dorsal comb (width 22 μ) with 8–9 teeth on each side ; second with about 11 and the third with about 12 sharp, triangular, well-separated teeth ; the fourth with 15–16 teeth. Although smaller this pattern is very similar in general appearance to that of *C. odibilis* (width 29 μ). *Thoracic Markings.*—Prothorax narrow lateral bars joined across the dorsum by a diffused band, which is less pronounced and particulate than in *C. heliophilus*, being only weakly developed at the start of the instar and becoming progressively more obvious towards pupation. Mesothorax with paired, short, broad, lateral bodies and metathorax with longer, narrower, lateral bars.

Third Instar.—Transverse prothoracic band often absent or but weakly developed. Head 124 μ by 77 μ and 55 μ wide at oral ring, H.R. 1·63.

Adults Reared 1948–51 ; 42♂♂, 61♀♀. In view of the close similarity between the females of *C. cubitalis* and *C. pallidicornis* the specific determination was made on the male terminalia.

Sources of Material and Breeding Places.—Drumchapel, Lanarkshire ; Milngavie and Loch Lomond, Dumbartonshire ; Trossachs, Perthshire ; Balmaha and Kippen, Stirlingshire ; Glen Urquhart, Inverness-shire ; Strathgryfe, Renfrewshire, and

Chideock and East Fleet, Dorset, where it occupies a wide range of habitats varying from marshy ground in association with *C. pallidicornis* to muddier swamps with *C. odibilis* and, rather unexpectedly, it appears to be a normal member of the benthic fauna of Loch Lomond. Dr. A. C. J. Weerekoon submitted five *Culicoides* larvae for identification taken among *Isoetes* sp. at a depth of 3–4 metres in Loch Lomond. They were inseparable from *C. cubitalis* with mean head measurements and 95 per cent. fiducial intervals of 172 μ±5 ; 109 μ±3, and 77 μ±2 ; compared with 166 μ±1 ; 104 μ±1, and 74 μ±1 for terrestrial *C. cubitalis*. On rearing 1♂ *C. cubitalis* emerged.

Culicoides pictipennis (Staeger) (Plate XVI).

Fourth Instar.—Head 243 μ by 148 μ, H.R. 1·67, pale straw ; mandibles pale amber, oral ring (109 μ) pale brown and collar dark brown. *Epipharynx* (fig. 21 *a*) dorsal comb about 34 μ in width ; antero-lateral edges convex ; about eight nearly equal teeth on each side. The second comb with about four long, sharp, well-separated teeth and a minute tooth at each end. Third comb with about six long, sharp teeth. Fourth comb with about 19 long, sharp teeth. The membranous teeth on the lateral arms particularly long and clear. *Thoracic Markings.*—Prothorax with narrow lateral bars joined anteriorly by a narrow transverse bar and across the dorsum by a broad transverse band, which may be faint. Mesothoracic and metathoracic paired lateral bodies expanded anteriorly, but not joining in the mid-dorsal line. *C. pictipennis* bears a striking resemblance to *C. albicans*, except for the absence of the latter's characteristic pigmented ring in the posterior half of the prothorax.

Third Instar unknown.

Adults Reared 1♂.

Sources of Material and Breeding Places.—Milngavie, Dumbartonshire ; Monikie and Balgavies Loch, Angus ; Drumchapel, Lanarkshire and Balmaha, Stirlingshire where they occurred in marshy areas in association with *C. cubitalis* and *C. pallidicornis*.

Culicoides salinarius Kieffer (Plate XV).

Fourth Instar.—Head 228 μ by 157 μ, H.R. 1·45, yellowish amber with light brown mandibles and oral ring (108 μ), and a dark brown collar. *Epipharynx* (fig. 21) having dorsal comb (width 36 μ) with 9–10 teeth on each side ; second almost semicircular with about eight sharp, well-separated teeth ; third with about 11 sharp, well-separated teeth ; the fourth with about 28 long, sharp, narrow teeth. *Thoracic Markings.* Prothorax covered with a superficial layer, which, being denser at the anterior and posterior borders, forms a pair of transverse bars, of which the anterior is the better developed. Neck almost but not entirely unpigmented. Mesothoracic and metathoracic paired lateral bodies very obvious although both segments have a thin superficial pigment layer which is more heavily developed anteriorly. Also, the thoracic pigmentation is most heavily developed in the prothorax, less so in the mesothorax and only lightly so in the metathorax. Thoracic markings continued anteriorly on to the ventral surface as broad transverse bands. *Abdominal Markings* (Pl. XV). Fourth instars, which have been kept in the laboratory some time (>2 months), developed abdominal markings. At first they consist of small yellow-brown V-shaped markings, with their apices directed posteriorly, which develop in the anterior half of each segment where the mid-dorsal and mid-ventral lines cross the intersegmental boundaries. Each V mark is an apodeme on which a pair of abdominal muscles are inserted. Later narrow strips of pigment extend outwards along the intersegmental boundary until they encircle the body, when they may widen and become very prominent. The constituent particles are so large and coarse that they appear like debris acquired from the medium. These markings have not been observed in wild caught larvae.

Third Instar very similar to fourth but abdominal markings absent. Head 158 μ by 109 μ and 72 μ wide at oral ring, H.R. 1·45.

Second Instar lacking abdominal markings. Thoracic markings reduced to a transverse prothoracic band and paired lateral mesothoracic and metathoracic bodies. Head 110 μ±4 by 76 μ±3 and 50 μ ±2 wide at oral ring, H.R. 1·45±0·07 (10 larvae).

Adults Reared 43♂♂, 23♀♀ and 3♀♀ *C. halophilus* (accidental introductions).

Source of Material and Breeding Places.—Beauly, Inverness-shire where it occurred in very large numbers (>1,000 per sq. yd.). This density is particularly surprising because of the large area of potential breeding ground. Larvae (predominantly third instar) and some pupae were found in the surface layer of a mud-covered salt flat, bearing scattered clumps of sea aster (*Aster tripolium*). Samples were taken at noon and the area revisited at 7 p.m. when it was found to be under about 2 ft. of brackish water and, very surprisingly, we were attacked only by *C. halophilus* of which very few larvae had been found.

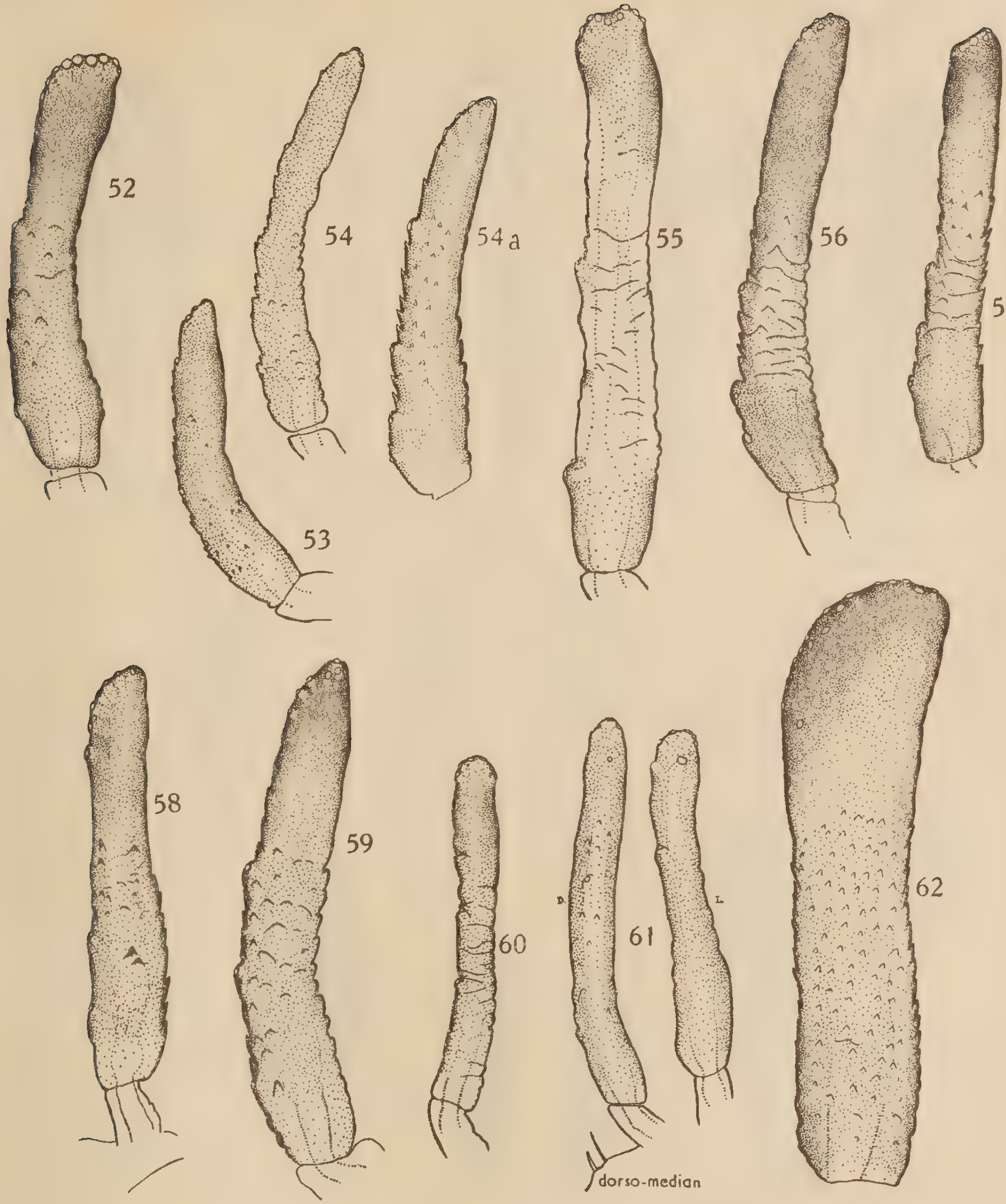
Notes.—The British Museum possesses material of *C. salinarius* (Westphalia 1922, 478–8, Thienemann) and *C. punctatidorsum* [=*C. salinarius* according to Edwards (1939) Holstein, 1922, 478–9, Thienemann]. There was a large and small larva in each series and a *Tetraphora* (=*Dasyhelea*) larva in the *C. salinarius* tube. It was assumed at first that they represented third and fourth instars, but closer examination showed that the larger larvae had massive pharynges of the *C. nubeculosus* type, while the smaller had the less sclerotised type. Moreover one of the " third " instars was nearing pupation. Clearly the large and small larvae are not related. The smaller larvae agreed with the description given above and one had abdominal markings. Their head sizes were very similar, averaging 226 μ, 148 μ and 109 μ compared with 228 μ, 157 μ and 108 μ for *C. salinarius*.

The pharynges of these two smaller larvae differ not only from those described here but also from each other. (i) Westphalia—Dorsal comb (width 25 μ) with 7–9 teeth on each side ; second and third with 7 and 10 long, sharp teeth respectively ; the fourth with 12 triangular teeth. (ii) Holstein—Dorsal comb (width 35 μ) with 9 teeth on each side ; second with 5 long, sharp, rather widely separated teeth ; third with 9 long, sharp, well-separated teeth ; the fourth with 16 triangular teeth. Both of these differ from that described above for *C. salinarius* in having only about half the number of teeth on the fourth comb. The Westphalian specimen also differs in being much narrower across the dorsal combs. The pharynges of the larger larvae are described under *C. nubeculosus*.

Culicoides circumscriptus Kieffer (Plate XV).

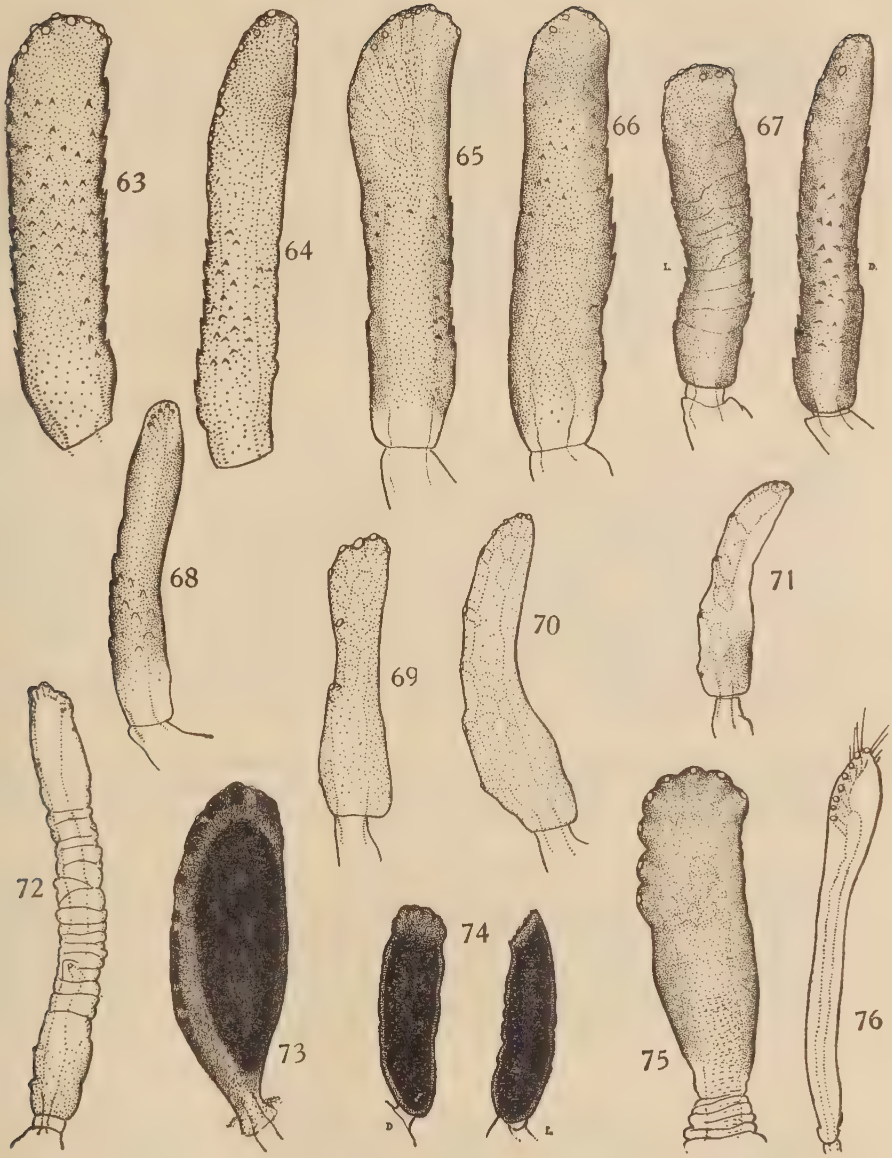
Fourth Instar.—*Head* 234 μ by 164 μ, H.R. 1·42, yellowish brown with light brown mandibles and oral ring (111 μ), and dark brown collar. *Epipharynx* (fig. 22) closely resembles that of *C. salinarius* (Beauly). Dorsal comb (width 35 μ) with 9–12 teeth on each side, the innermost ones tending to overlap ; second with 8 well-defined teeth ; third with 11 well-defined teeth ; the fourth with 20–24 teeth, not so well defined. It should be noted that there is not the multiplicity of rows of teeth figured by Tokunaga (1937). *Thoracic Markings* very similar to *C. salinarius* and therefore they will not be described in detail but there is a difference in the mesothorax, where the pigmentation is divided into two parts, a postero-median diamond-shaped patch and a larger lateral and antero-median area, the two being separated by a narrow unpigmented zone. This arrangement is very obvious in most fourth instar *C. circumscriptus* but it is also seen, usually less distinctly, in *C. salinarius* and most infrequently in *C. odibilis*. *Abdominal Markings* absent.

Third Instar unknown.


52
54
54a
53
55
56
57
58
59
60
D.
61
L.
62
dorso-median

PUPAE. PROTHORACIC RESPIRATORY HORN

FIG. 52. *C. fascipennis.*
FIG. 53. *C. pallidicornis.*
FIG. 54. *C. cubitalis.*
FIG. 54a. *C. pictipennis.*
FIG. 55. *C. circumscriptus.*
FIG. 56. *C. salinarius.*
FIG. 57. *C. odibilis.*
FIG. 58. *C. maritimus.*
FIG. 59. *C. simulator.*
FIG. 60. *C. heliophilus.*
FIG. 61. *C. cunctans,* dorsal and lateral views; the dorsal view also showing the dorso-median setae.
FIG. 62. *C. lupicaris.*



PUPAE. PROTHORACIC RESPIRATORY HORN

FIG. 63. *C. grisescens.*
FIG. 64. *C. delta.*
FIG. 65. *C. pulicaris.*
FIG. 66. *C. punctatus.*
FIG. 67. *C. halophilus,* lateral and dorsal views.
FIG. 68. *C. impunctatus.*
FIG. 69. *C. obsoletus.*
FIG. 70. *C. scoticus.*
FIG. 71. *C. chiopterus.*
FIG. 72. *C. pseudochiopterus.*
FIG. 73. *Ceratopogon (Ceratopogon).*
FIG. 74. *Ceratopogon (Isohelea),* dorsal and lateral views.
FIG. 75. *Serromyia femorata.*
FIG. 76. *Stilobezzia ochracea.*

Adults Reared 10♂♂, 17♀♀.

Sources of Material and Breeding Places.—East Fleet, Dorset (6 larvae) and Dawlish, S. Devon (55 larvae—in material supplied by Mr. R. Hartland-Rowe). At East Fleet where it was associated with *C. stigma* and *C. odibilis*, it breeds in mud devoid of vascular vegetation near brackish water, but at Dawlish it occurred on its own, a difference which may be due to salinity.

Notes.—At Chideock, Dorset, some larvae resembling *C. circumscriptus* were found in farmyard mud in association with *C. stigma* and *C. nubeculosus*, but their heads were smaller (228 μ±9 ; 160 μ±8 and 108 μ±3) ; the characteristic mesothoracic markings were less distinct and abdominal markings were present in late fourth instars. These usually took the form of pigmented apodemes but occasionally there were additional transverse bars. When reared, these larvae gave rise to atypical *C. circumscriptus* (18♂♂, 11♀♀) in which the lower branch of the cubital fork was mostly in a dark area.

Culicoides odibilis Austen (Plate XV).

Fourth Instar.—*Head* 190 μ by 137 μ, H.R. 1·39, pale straw ; mandibles, collar and oral ring (86 μ) light brown ; similar to but smaller and paler than *C. circumscriptus* and *C. salinarius*. *Epipharynx* (fig. 23) resembles that of *C. cubitalis* but larger, the dorsal comb being 29 μ wide compared with 22 μ. It has 8–9 teeth on each half ; second comb with about 19 long, sharp teeth ; third with about 16 long, sharp teeth ; the fourth with about 15 long, sharp, triangular teeth. *Thoracic Markings.* Each segment with an anterior transverse bar, which is extended on to the ventral surface, a broad transverse band and in the mesothorax and metathorax paired lateral bodies. These markings are similar to those of *C. salinarius* and *C. circumscriptus* but only in one collection (from Kippen) was a mesothoracic diamond-shaped patch present. *Abdominal Markings* only present in one collection (from Kippen).

Third Instar markings less developed than fourth ; transverse bar always present in prothorax and mesothorax but the bands are less constant ; metathoracic band absent and bar rudimentary. Head 139 μ by 90 μ and 63 μ wide at oral ring, H.R. 1·54.

Adults Reared 47♂♂, 50♀♀ and 1♂, 1♀ *C. cubitalis* (accidental introductions).

Sources of Material and Breeding Places.—Drumchapel, Lanarkshire ; Balmaha and Kippen (their peculiar features are detailed above), Stirlingshire ; Milngavie, Dumbartonshire ; Bridge of Weir and Strathgryfe, Renfrewshire ; Auchteraw and Strathglass, Inverness-shire, and East Fleet and Chideock, Dorset. *C. odibilis* is abundant in swampy ground bearing little vegetation and large expanses of open mud, where it is often associated with *C. stigma*, *C. circumscriptus* and *C. cubitalis*.

Culicoides maritimus Kieffer (Plate XVI).

Fourth Instar.—*Head* similar to but larger than *C. heliophilus* ; 225 μ by 140 μ, H.R. 1·61 ; pale straw ; mandibles, collar and oral ring (105 μ) light brown. *Epipharynx* (fig. 24) having dorsal comb (width 30 μ) with 6–7 long, sharp, triangular teeth on each side ; second with about 7 sharp, well-separated teeth ; third with about 10 sharp, well-separated teeth ; the fourth with about 21 long, sharp teeth. *Thoracic Markings* conspicuous broad transverse bands across the anterior half of each segment. This species bears some resemblance to *C. odibilis* but the latter has additional transverse bars and less conspicuous bands.

Third Instar very similar to fourth except that the mesothoracic and metathoracic bands are less well developed. Head 159 μ by 96 μ and 75 μ wide at oral ring, H.R. 1·66.

Second Instar with only prothoracic band present. Head 109 μ by 64 μ and 51 μ wide at oral ring, H.R.1·71 (2 larvae).

Adults Reared 1949–51 ; 12♂♂, 9♀♀.

Sources of Material and Breeding Places.—Arrochar, Argyllshire ; Abbotsbury, Dorset and Portsmouth, Hampshire [British Museum (Natural History), Miss L. Selwood, 1934]. A small area (about 150 sq. yds.) of *Scirpus maritimus* in a salt marsh at Arrochar was found to be teeming with *C. maritimus* (density 2,000–2,500 per sq. yd.) and an occasional *C. halophilus*. At Abbotsbury the larvae were found in a small shallow, open, brackish pool lined with a thin layer of decaying vegetation and containing hundreds of planarians (? *Automesostoma* sp.). We are indebted to Dr. H. D. Slack for this identification.

Culicoides simulator Edwards.

Fourth Instar.—Head 205 μ by 148 μ, H.R. 1·39, and 98 μ wide at oral ring ; pale straw ; mandibles and oral ring pale brown and collar dark brown ; similar in size and shape to *C. truncorum*. *Epipharynx* not examined. *Thoracic Markings.*—Prothorax covered with an indistinct brownish pigmented layer with a small amount extending on to the " neck ". Mesothoracic lateral bodies expanded anteriorly and united in the mid-dorsal line to form a transverse band leaving the postero-median portion of the segment unpigmented. Metathoracic paired lateral bodies only faintly pigmented and not expanded. These markings have the same pattern as *C. vexans* but in the latter the pigmentation particularly in the prothorax is very much brighter and more distinct.

Third Instar unknown.

Adult Reared 1♂.

Source of Material and Breeding Place.—Abbotsbury, Dorset (1 larva) where it was associated with *C. vexans* and *C. pulicaris* (for further details see *C. vexans*).

Culicoides heliophilus Edwards (Plate XVII).

Fourth Instar.—Head—Similar to but larger than *C. cubitalis* ; 191 μ by 115 μ ; H.R. 1·66 ; pale straw ; mandibles, collar and oral ring (85 μ) light brown. *Epipharynx* (fig. 25) having dorsal comb (width 37 μ) with 6–7 teeth, some of which are relatively large, on each side ; second with about 8 relatively large, sharp teeth ; third with about 12 long, sharp, well-separated teeth ; the fourth, truncated anteriorly, with about 13 triangular teeth. *Thoracic Markings.*—Prothorax with narrow lateral pigmented bars connected by a broad, curved transverse band, which is more distinct and granular than *C. cubitalis* and obvious in all fourth instars. Mesothorax and metathorax with long, lateral, narrow pigmented bars.

Third Instar.—Prothoracic transverse band less developed but always distinct ; mesothoracic bodies rounded ; head 136 μ by 80 μ and 62 μ wide at oral ring, H.R. 1·69.

Adults Reared 1949–51 ; 21♂♂, 16♀♀.

Sources of Material and Breeding Places.—Milngavie and Loch Lomond, Dumbartonshire ; Trossachs, Perthshire ; Strathgryfe, Renfrewshire, and Glen Urquhart, Inverness-shire, where they breed in *Sphagnum* spp. in association with *C. impunctatus*, *C. albicans* and *Ceratopogon* (*Isohelea*).

Notes.—A most striking characteristic of living *C. heliophilus* larvae is that of all the larvae described here, they alone float inactive on the surface of water. As a result of this property they tend, when sucked into a pipette, to adhere to its sides. Although rather trifling, this character is most useful in separating *C. heliophilus* larvae from the very similar *C. cubitalis*.

A Note on the Larvae of *C. cunctans* and the *C. pulicaris* Group.

The larvae of *C. cunctans* and the *C. pulicaris* group are very similar to each other so that their ranges of variation overlap and it is often impossible to determine a specimen with certainty. No difficulty, however, should be experienced in identifying the larva of *C. lupicaris*, which has a larger head than the others and quite different thoracic markings. Also, the larva of *C. impunctatus* is fairly readily separated from the others by its characteristic head colour and the poor development of its prothoracic markings. The other species *C. cunctans*, *C. punctatus*, *C. halophilus*, *C. pulicaris*, *C. delta* and *C. grisescens* are all very much alike having amber-coloured heads, prothoracic markings, which consist of paired lateral bars with an irregular antero-central patch and mesothoracic bodies, which are expanded anteriorly (except *C. cunctans* ?) but do not fuse in the mid-dorsal line.

The chief differences between these species are head size, the extent of the prothoracic patch and their breeding sites. Thus *C. halophilus* is the only one found in brackish water. On head size *C. cunctans*, *C. punctatus* and *C. halophilus* are inseparable from each other but can be separated from most *C. pulicaris* and all *C. delta* and *C. grisescens*. Also although *C. delta* and *C. grisescens* have larger heads than *C. pulicaris* their ranges overlap.

There is variation in the development of the prothoracic patch, which is relatively small in *C. cunctans* and *C. punctatus*, larger in *C. pulicaris* and even more so in *C. halophilus*, *C. delta* and *C. grisescens*. Usually the prothoracic patch is irregular in shape but in *C. cunctans* it tends to have a more definite outline, being triangular with the apex directed posteriorly. The prothoracic patch of *C. grisescens* differs from the rest in being irregularly triangular with the apex directed anteriorly.

To sum up, the larvae of *C. lupicaris*, *C. impunctatus* and *C. grisescens* (?) can be identified with certainty. (Too few larvae of *C. grisescens* have been seen to be definite on this point but it is of interest to note that, when they were first found, they were immediately segregated as something different.) *C. delta* will tend to be confused with *C. pulicaris* and *C. punctatus* with *C. cunctans*. Although an arbitary separation on head length enables most *C. pulicaris* to be separated from *C. punctatus* and *C. cunctans* it is not absolute. *C. cunctans* can be separated from *C. punctatus* by the possession of a median tooth on the epipharynx.

Culicoides cunctans (Winnertz).

Fourth Instar.—Head 230 μ by 158 μ ; H.R. 1·45 ; rich amber with an unsclerotised ventral suture. Collar, mandibles and oral ring (108 μ) dark brown. *Epipharynx* (fig. 26) having dorsal comb (width 33 μ) with a small thin median tooth and about 9 sharp teeth of varying sizes on each side, the second and third from the mid-line on each side being the largest ; 2nd comb with 10–12 long, thin teeth ; in the specimen illustrated there is an additional short median row of about 6 smaller teeth immediately anterior to the second comb ; third with about 20 long, thin teeth ; the fourth with its anterior edge rounded and about 14 triangular-shaped teeth, some of them smaller than the rest. *Thoracic Markings* paired, lateral, longitudinal bars in all three segments and, on the front margin of the prothorax, a well-developed triangular patch with its apex directed posteriorly. This larva appears to differ from *C. punctatus* by the more definite shape of its prothoracic patch and the lack of inward extensions to the anterior ends of the mesothoracic and metathoracic lateral bodies, but the amount of variation in these characters has still to be determined.

Third Instar unknown.

Adults Reared 1950–51 ; 4♂♂, 1♀.

Sources of Material and Breeding Places.—Balmaha, Stirlingshire and Drumchapel, Lanarkshire (1 larva), where it breeds in marshy areas dominated by *C. cubitalis* and *C. pallidicornis.*

Culicoides lupicaris Downes & Kettle (Plate XV).

Fourth Instar.—*Head* 322 μ by 192 μ ; H.R. 1·68 ; muddy brown. Mandibles and oral ring (123 μ) dark brown, collar dark brown to black. *Epipharynx* (fig. 27) with dorsal comb (width 43 μ) almost semicircular in shape with 14–16 teeth on each half ; second with about 16 teeth and third about 18 ; the fourth, slightly bilobed, with a relatively wide, more sclerotised posterior border and about 23 teeth ; its ventral surface, slightly nodular, reminiscent of the heavily sclerotised median block of the *C. nubeculosus* group. *Thoracic Markings.*—Prothorax covered with a diffuse band ; mesothoracic paired bodies expanded anteriorly to join in the mid-dorsal line, from which there arises a thin-posteriorly branching network ; metathoracic bodies expanded anteriorly but not fused.

Third Instar same as fourth, but head 208 μ by 125 μ and 84 μ wide at oral ring, H.R. 1·67.

Adults Reared 1950–51 ; 5♂♂, 7♀♀.

Sources of Material and Breeding Places.—Drumchapel, Lanarkshire (source of types) ; Milngavie, Dumbartonshire ; Balmaha, Stirlingshire ; Strathglass and Glen Urquhart, Inverness-shire, where it breeds in muddy swamps, more or less devoid of obvious vegetation, in association with *C. stigma* and *C. odibilis.*

Culicoides grisescens Edwards

Fourth Instar.—*Head* 294 μ by 180 μ ; H.R. 1·63 ; amber ; mandibles, collar and oral ring (137 μ) dark brown to black. *Epipharynx* not examined. *Thoracic Markings.*—Prothorax with paired narrow lateral bars and a large, irregularly triangular antero-median patch, which broadens posteriorly so that it nearly meets the lateral bars and gives the appearance of a transverse band. This differentiates *C. grisescens* from all closely related larvae in which this patch either narrows posteriorly or is roughly rectangular. Mesothoracic and metathoracic lateral bodies expanded anteriorly but not fused. Metathoracic pigmentation faint.

Third Instar unknown.

Adults Reared 3♂♂, 2♀♀.

Source of Material and Breeding Places.—Loch Achray, Perthshire, and Slipperfield, Peebles-shire, in the marshy margin among various species of *Carex* and in association with *C. fascipennis.*

Culicoides delta Edwards

Fourth Instar.—*Head* 278 μ by 173 μ ; H.R. 1·61 ; amber with dark brown to black mandibles, oral ring (116 μ) and collar. *Epipharynx* not examined. *Thoracic Markings.*—Prothorax with paired narrow lateral bars and a large irregularly rectangular antero-median patch, which is larger than that of *C. pulicaris* and differently shaped from that of *C. grisescens.* Mesothoracic and metathoracic lateral bodies expanded anteriorly but not fused. Metathoracic pigmentation faint.

Third Instar unknown.

Adults Reared 4♀♀.

Sources of Material and Breeding Places.—Balmaha, Stirlingshire (2 larvae) and Strathgryfe, Renfrewshire (4 larvae) in wet areas of moorland bearing *Juncus articulatus* (s. lat.) but no *Sphagnum* spp. This should be compared with the breeding places of *C. impunctatus* which is found among *J. articulatus* and *Sphagnum.*

Culicoides pulicaris (L.) (Plate XVII).

Fourth Instar.—Head 256 μ by 168 μ ; H.R. 1·53 ; pale amber at start of instar but darkening with age to a rich, deep amber ; in fully pigmented larvae, mandibles and oral ring (112 μ) dark brown, collar dark brown to black, but in young larvae these areas are lighter. *Epipharynx* (fig. 28) very similar to *C. punctatus*, having dorsal comb (width 41 μ) with about 16 teeth on each side, the lateral and median teeth smaller, the antero-lateral edges concave ; second comb a crescent of about 15 small teeth ; third with about 19 teeth ; the fourth with about 20 teeth and slightly bilobed. *Thoracic Markings.* Prothorax with paired lateral bars with an irregular antero-central patch, which, although relatively small and rectangular, is frequently divided into two short, parallel, transverse bars and, on occasions, there may be an additional postero-central patch ; rarely the prothorax may have small pigment spots. In early instars these markings may be faint or absent. Mesothoracic and metathoracic lateral bodies expanded anteriorly towards the mid-dorsal line.

Third Instar resembles fourth but thoracic markings less developed. Head 183 μ by 116 μ, H.R. 1·57, and 80 μ wide at oral ring, being larger and darker than third instar *C. punctatus.*

Adults Reared 1949–51 ; 9♂♂, 16♀♀ ; 1♂, 2♀♀ *C. delta* and 1♂, 1♀ *C. punctatus*. The specimens of the last two species, in all probability, were not introduced in the medium but were the result of mistaken identification.

Sources of Material and Breeding Places.—Drumchapel, Lanarkshire ; Milngavie, Dumbartonshire ; Auchteraw, Inverness-shire ; Balmaha, Stirlingshire ; Abbotsbury, Dorset, where it was associated with *C. vexans* (for a description see p. 435). In Scotland it is found in both marshes inhabited by *C. cubitalis* and *C. pallidicornis* and muddier swamps dominated by *C. odibilis.*

Notes.—Goetghebuer (1919) described the larva of *C. pulicaris* as possessing two long and two shorter bristles at the posterior end of the body. This record is unique, as no other *Culicoides* larva has been described with long perianal bristles. In correspondence, however, Dr. Goetghebuer admitted that he never actually reared adult *C. pulicaris* from these bristled larvae, but found them in the same breeding place where earlier he had obtained *C. pulicaris* pupae. It seems clear now that the larvae and pupae were not related.

Culicoides punctatus (Meigen) (Plate XVII).

Fourth Instar.—Head 234 μ by 155 μ, H.R. 1·51, with an unsclerotised ventral suture ; pale amber at start of instar but darkening to a rich, deep amber ; mandibles and oral ring (106 μ) dark brown and collar dark brown to black in fully pigmented larvae. *Epipharynx* (fig. 29) very similar to *C. pulicaris.* Dorsal comb (width 42 μ) almost semicircular in outline with antero-lateral edges concave and 13–14 teeth on each side, of which the two nearest the mid-line and the 3 or 4 most lateral are smaller than the rest ; second comb crescentic with about 17 long, fine teeth ; third with about 20 teeth ; the fourth, bilobed the lateral ends curving forwards so that it is roughly heart-shaped, with about 20 long, fine teeth. A larva identical with that described above in general appearance had an epipharynx very closely similar but measuring only 38 μ wide. *Thoracic Markings* same as those of *C. pulicaris* with the same amount of variation (see above).

Third Instar similar to fourth but prothoracic markings less evident and indeed often absent. Head 160 μ by 104 μ, H.R. 1·55, and 78 μ wide at oral ring, smaller and paler than *C. pulicaris.*

Adults Reared 1948–51 ; 5♂♂, 2♀♀, 1♂, 1♀ *C. punctatus* (?), 1♀ *C. cunctans* and 1♀ *C. pulicaris*. The last two adults were the result of mistaken larval identification ;

the (?) *C. punctatus* were adults which had some *C. pulicaris* characters but were predominantly *C. punctatus*.

Sources of Material and Breeding Places.—Drumchapel, Lanarkshire ; Milngavie, Dumbartonshire ; Strathglass and Glen Urquhart, Inverness-shire where, like *C. pulicaris*, they occur in marshes and muddy swamps with *C. cubitalis*, *C. pallidicornis* and *C. odibilis*.

Culicoides halophilus Kieffer (Plate XVII).

Fourth Instar.—Head 242 μ by 163 μ, H.R. 1·48, with a posterior ventral suture ; rich reddish brown ; mandibles, collar and oral ring (109 μ) dark brown. *Epipharynx* (fig. 30) having dorsal comb (width 37 μ) nearly semicircular with about 12 teeth on each side and a single median tooth ; second with about 7 small teeth ; third with 11 rather long, thin teeth ; the fourth, slightly bilobed, with about 19 teeth. *Thoracic Markings.*—Prothorax with paired, broad, lateral bars and a large irregular, antero-median patch. Mesothoracic and metathoracic paired lateral bodies expanded anteriorly to meet in the mid-dorsal line.

Third Instar with prothoracic markings less well-developed than in the fourth. Mesothoracic bodies without centrally directed extensions. Metathoracic bodies extend inwards anteriorly, but do not meet. Head 170 μ by 109 μ and 80 μ wide at oral ring. H.R. 1·56.

First Instar head 85 μ by 50 μ (1 larva). Prothoracic pseudopod absent.

Adults Reared 5♂♂, 6♀♀.

Sources of Material and Breeding Places.—Arrochar, Argyllshire ; Beauly, Inverness-shire and Abbotsbury, Dorset. Found in shallow, muddy, brackish pools, filled by seepage at high tide and lined with decaying vegetable material, at Arrochar and Abbotsbury with *C. maritimus*, while at Beauly they occurred in a muddy salt flat with *C. salinarius*.

Culicoides impunctatus Goetghebuer (Plate XVII).

Fourth Instar.—Head 235 μ by 147 μ ; H.R. 1·60 ; dull, muddy brown ; mandibles, collar and oral ring (105 μ) dark brown. *Epipharynx* (fig. 31), Scottish specimen. Dorsal comb (width 34 μ) almost semicircular with 12–15 teeth on each half ; second with about 13 small, irregular teeth ; third with about 8 sharp, triangular teeth ; the fourth (rather short from back to front) with about 9 large teeth. Through the courtesy of Miss E. W. Roberts it has been possible to examine the epipharynx of a specimen of *C. impunctatus* preserved and described by Hill (1947) ; it (fig. 32) compares reasonably well with the Scottish specimen, both in size (35 μ wide) and in pattern. Apart from small variations in the number of teeth, the only apparent difference is the presence in Hill's specimen of minute teeth on each side of the third comb. A comparison of the figure given here for this specimen with the figure given by Hill for the " hypopharynx " of *C. impunctatus* shows clearly the loss of detail to be expected when this structure is examined in the entire larva. *Thoracic Markings.*—Prothorax, paired, narrow, lateral bars with an irregular, antero-central patch, which is usually absent in early fourth instars but may become distinct later. Mesothorax and metathorax with the usual paired lateral bodies.

Third Instar similar to fourth except that the prothoracic markings are either very poorly developed or more usually absent. Head 169 μ by 100 μ and 76 μ wide at oral ring, H.R. 1·69.

Second Instar.—Head 118 μ±5 by 71 μ±4 and 55 μ±5 wide at oral ring, H.R. 1·68±0·10 (20 larvae), straw coloured, markedly lighter than in later instars. Prothoracic markings absent.

Culicoides obsoletus (Meigen) (Plate XIV).

Fourth Instar.—Head 170 μ by 123 μ, H.R. 1·38, amber ; mandibles, collar and oral ring (92 μ) dark brown. *Epipharynx* (fig. 33) with only three combs. Dorsal comb (width 25 μ) with about 8 teeth on each side ; second apparently absent ; third with about 6 teeth ; the fourth, roughly square, with about 6 teeth. *Thoracic Markings.*—Paired lateral pigmented bodies in all thoracic segments. Unlike nearly all other *Culicoides* larvae, the prothoracic bodies are very similar to those in the mesothorax and metathorax ; posteriorly they tend to turn inwards. Some larvae (in one sample 3/24=12 per cent.) with a short, broad, curved antero-median spot.

Third Instar markings as in fourth. Head 130 μ by 89 μ and 67 μ wide at oral ring, H.R. 1·46.

First Instar reared from eggs by Mr. A. H. Parker (private communication). Prothoracic pseudopod with 3 pairs of relatively strong hooks, 4 successive median rows of teeth and 2 pairs of lateral rows of teeth (fig. 41).

Adults Reared 24♂♂, 29♀♀, 1♂, 1♀ *C. pallidicornis* and 1♂ *C. cubitalis* (last two were accidental introductions). In view of the existence of closely related species, the terminalia of the reared males were examined and all agreed with Edwards' (1939) figure for *C. obsoletus.*

Sources of Material and Breeding Places.—Luss and Milngavie, Dumbartonshire ; Balmaha, Stirlingshire and Drumchapel, Lanarkshire where they occur equally frequently, but never in large numbers, in moorland sites with *C. impunctatus* and in marshes with *C. cubitalis* and *C. pallidicornis.*

Culicoides scoticus Downes & Kettle (Plate XIV).

Fourth Instar.—Head 151 μ by 119 μ ; H.R. 1·27 ; pale yellow ; mandibles, collar and oral ring (72 μ) pale amber. *Epipharynx* (fig. 34) with only three combs ; dorsal one (width 20 μ) with a single thin median tooth and about 8 teeth on each half ; second with about 7 teeth ; third with about 4 teeth ; the fourth apparently absent. *Thoracic Markings.*—Only one larvae, nearing pupation, examined. Prothorax and mesothorax unmarked. If this is confirmed *C. scoticus* will be unique among the *Culicoides* larvae described here, because so far the absence of paired lateral mesothoracic bodies has only been observed as a very rare abnormality. Paired lateral metathoracic bands enlarged at each end, and laterally concave, no doubt on account of the nearness of pupation.

Third Instar unknown.

First Instar.—Head 76 μ by 58 μ, oral ring (40 μ). Prothorax as in first instar *C. obsoletus* bears a pseudopod (fig. 42), with 3 pairs of hooks, but only two median rows of fine teeth.

Adults Reared 7♂♂, 3♀♀.

Source of Material.—In September 1948, eggs were obtained from a wild caught gravid female. At room temperature (about 15°C.) they hatched in 3–5 days. Twelve days later the larvae pupated and adults emerged from the pupae in 6–7 days. Duration of life cycle 21–24 days.

Breeding Places unknown.

Culicoides chiopterus (Meigen) (Plate XIV).

Fourth Instar.—Head 115 μ by 99 μ ; H.R. 1·16 ; yellow with light brown mandibles, oral ring (61 μ) and collar. *Epipharynx* (fig. 35) with only two combs—dorsal and ventral. Dorsal comb (width 19 μ) with about 10 teeth on each side ; the ventral, parallel-sided and rather longer than broad with about 5 relatively large teeth. *Thoracic Markings* very similar to *C. obsoletus.* Prothorax with paired lateral bodies turned inwards posteriorly ; antero-median curved spot often present and sometimes joined to lateral bodies by a pigment strand ; mesothoracic lateral bodies less pigmented and metathoracic bodies only faintly so.

Third Instar unknown.

Adults Reared 20♂♂, 38♀♀.

Sources of Material and Breeding Places.—Glen Clova, Angus ; Drumchapel, Lanarkshire ; Auchteraw, Inverness-shire and Harpenden, Hertfordshire (material supplied by Mr. B. R. Laurence). Breeding in association with *C. pseudochiopterus* in cow dung left lying naturally in the field, where they may be present in such large numbers that once 252 larvae were recovered from 3 pads of dung.

Culicoides pseudochiopterus Downes & Kettle (Plate XIV).

Fourth Instar.—*Head* 160 μ by 121 μ ; H.R. 1·33 ; amber ; mandibles, oral ring (79 μ) and collar dark brown. Very similar to *C. obsoletus* but slightly smaller. *Epipharynx* (fig. 36) with 2 combs, closely resembles *C. chiopterus*, but ventral comb wider and with more teeth. Dorsal comb (width 20 μ) with about 10 teeth on each half ; ventral with about 12 teeth. *Thoracic Markings* of same pattern as *C. obsoletus* and *C. chiopterus* with their characteristically shaped paired lateral prothoracic bodies, but pigmentation very faint and may be overlooked.

Third Instar unknown.

Adults Reared 2♂♂.

Sources of Material and Breeding Places.—Glen Clova, Angus ; Drumchapel, Lanarkshire ; and Harpenden, Hertfordshire (material supplied by Mr. B. R. Laurence). Breeding in association with *C. chiopterus* in cow dung lying naturally in the field.

Notes.—In one specimen each of the paired setae " *s* ", just in front of the eye and outside the frontal suture, was multiple ; *i.e.*, 2 or 3 setae arose from one base. This feature is interesting in view of the absence of similar multiple setae from the head of other species of *Culicoides* and their presence in *Ceratopogon* (*Ceratopogon*), *Ceratopogon* (*Isohelea*) and *Stilobezzia*.

DESCRIPTIONS OF LARVAE OF OTHER GENERA.

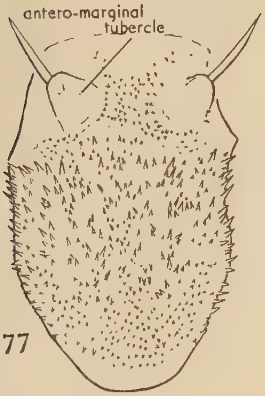
Ceratopogon (Ceratopogon) spp. (Plate XVIII).

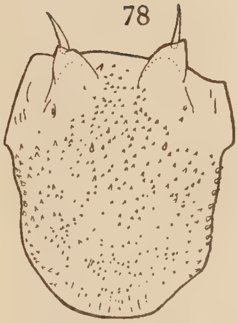
Fourth Instar.—*Head* amber ; approximately 260 μ by 155 μ and 115 μ wide at oral ring—not quite so large as *Stilobezzia* spp. and with an unusually large range due to its multispecific identity. A long, well sclerotised and pigmented posterior ventral suture, quite different in appearance from the unsclerotised and unpigmented suture found in some *Culicoides*. Seta " *s* " is multiple, a feature found in *Culicoides* only in one specimen of *C. pseudochiopterus*. Antennae resemble those of *Culicoides* in that they are not conspicuous as in *Ceratopogon* (*Isohelea*) and *Stilobezzia*. *Epipharynx* (fig. 37) different from the usual form in *Culicoides* and also from *Ceratopogon* (*Isohelea*). Three combs—dorsal (width 30 μ) with a very large single, median tooth and 6–7 teeth on each side ; intermediate comb in two parts each with 6–7 teeth ; ventral with 10 teeth. *Thoracic Markings.* Pigment absent, but paired translucent lateral bodies can be seen in the mesothorax and metathorax.

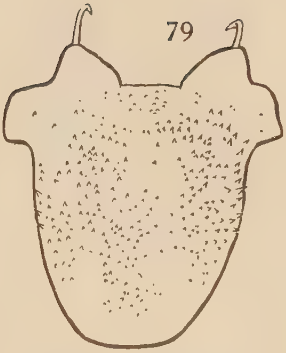
Third Instar resembles fourth. Head approximately 180 μ by 110 μ and 80 μ wide at oral ring.

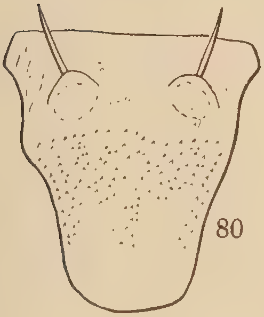
Second Instar very similar to third. Head approximately 125 μ by 75 μ and 55 μ wide at oral ring.

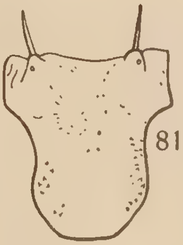
Adults Reared 3♂♂, 7♀♀ *Ceratopogon crassinervis* and 1♀ *C. niveipennis*.

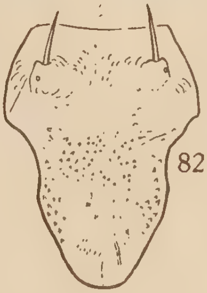

antero-marginal
tubercle
77

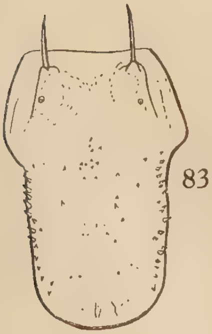


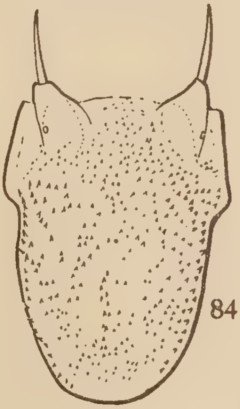


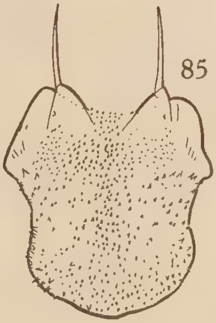






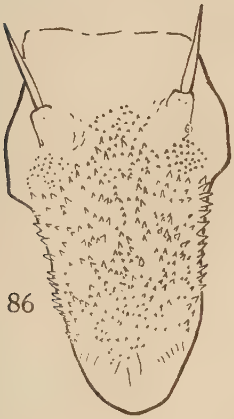






PUPAL OPERCULA

Fig. 77. *C. riethi.*
Fig. 78. *C. stigma.*
Fig. 79. *C. parroti.*
Fig. 80. *C. albicans.*
Fig. 81. *C. truncorum.*
Fig. 82. *C. pallidicornis.*
Fig. 83. *C. cubitalis.*
Fig. 84. *C. circumscriptus.*
Fig. 85. *C. salinarius.*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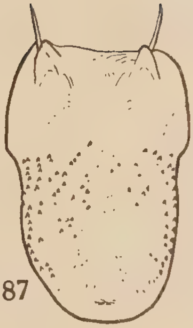
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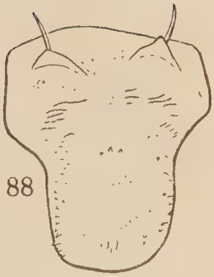
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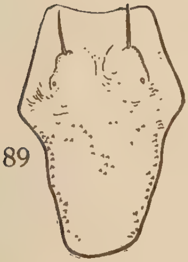
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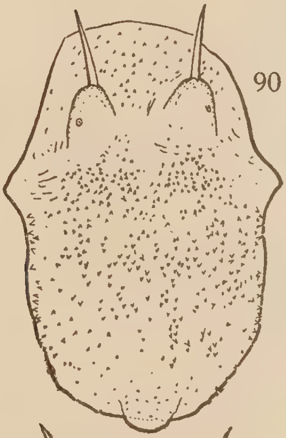
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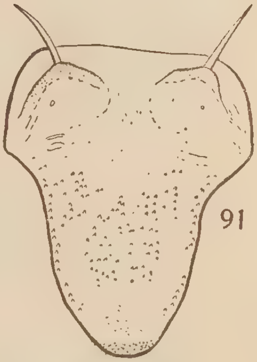
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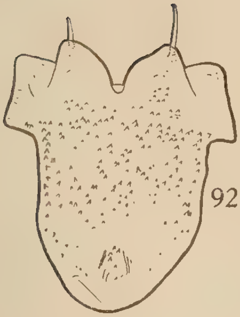
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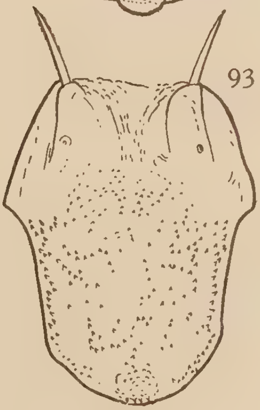
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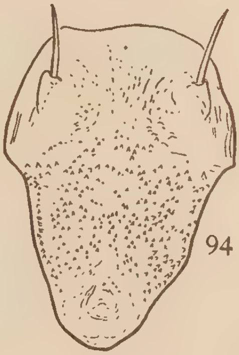
94

PUPAL OPERCULA

FIG. 86. *C. odibilis.*
FIG. 87. *C. maritimus.*
FIG. 88. *C. heliophilus.*
FIG. 89. *C. cunctans.*
FIG. 90. *C. lupicaris.*
FIG. 91. *C. delta.*
FIG. 92. *C. pulicaris.*
FIG. 93. *C. punctatus.*
FIG. 94. *C. halophilus.*

Sources of Material and Breeding Places.—Luss and Milngavie, Dumbartonshire ; Balmaha, Stirlingshire ; Drumchapel, Lanarkshire and Loch Winnoch, Renfrewshire. Like *Culicoides obsoletus* this species is present, but never abundant, in moorland with *C. impunctatus* and in marshes with *C. cubitalis* and *C. pallidicornis*.

Ceratopogon (**Isohelea**) spp. (Plate XVIII).

Fourth Instar.—*Head* showing wide variation in size and colour due to multispecific identity, but nevertheless it always has the typical *Culicoides* shape with angular anterior margin and head ratio of 1·5–1·8 (mean 1·6), compared with the long, narrow, pear-shaped head of *Bezzia, Palpomyia* etc., with its rounded anterior margin and head ratio of 2·0 or more. Differs from most *Culicoides* in having head setae "*x*" and "*s*" multiple (fig. 6) ; and a strongly sclerotised and pigmented posterior ventral suture (fig. 7). Antennae (fig. 6) much more prominent than in any *Culicoides*. *Epipharynx* (fig. 38) different, not only from the usual *Culicoides* form, but also from *Ceratopogon* (*Ceratopogon*). Dorsal comb (width 41 μ) with about 9 teeth on each half and no median tooth ; a very large almost semicircular plate, with a serrated edge, on each lateral arm, corresponding, presumably, to the separate sclerites found in the *C. nubeculosus* group and to the membranous teeth found in the rest of the *Culicoides*. *Thoracic Markings* extremely variable, sometimes pigmented and sometimes grey and translucent. *Anal Segment* differs from all larvae described here in the possession of a circlet of relatively stout, long, dark perianal bristles.

Earlier Instars.—First, second and third readily recognised by perianal bristles and head shape.

Adults Reared 1949–51 ; 33♂♂, 76♀♀ *Ceratopogon* (*Isohelea*) spp. and 2♂♂ *Culicoides impunctatus* (accidental introductions). Subgenus identification based on wing venation. Examination of 31 ♀ terminalia disclosed 24 *Ceratopogon nitidula*, 4 *C. perpusilla* and 3 *C. sociabilis*. No attempt was made to separate the larvae of these species although it should present no great difficulty.

Sources of Material and Breeding Places.—Glen Clova, Angus ; Trossachs, Perthshire ; Rowardennan and Balmaha, Stirlingshire ; Luss and Milngavie, Dumbartonshire ; Drumchapel, Lanarkshire ; and Strathgryfe and Loch Winnoch, Renfrewshire, where they occur, often in large numbers, in *Sphagnum* spp. with *Culicoides impunctatus*.

Notes.—These larvae are often recovered when searching for *Culicoides* because they have the same macroscopic appearance and swim very actively in the typical Ceratopogonid manner.

Stilobezzia ochracea (Winnertz), **Stilobezzia gracilis** (Haliday) (Plate XVIII).

Fourth Instar.—*Head* approximately 310 μ by 165 μ and 100 μ wide at oral ring ; darker than other larvae described here (*S. ochracea* darker than *S. gracilis*). Antennae (fig. 8) prominent as in *Ceratopogon* (*Isohelea*) and one of the setae of the paired group "*o*" is multiple. *Epipharynx* (fig. 39) different from *Culicoides* and the subgenera of *Ceratopogon*. Only two combs—dorsal and ventral—and a large toothed sclerite fused to each lateral arm, corresponding to the semicircular plate found in *Ceratopogon* (*Isohelea*). Dorsal comb (width 35 μ) with eight teeth on each half ; ventral longer than broad with a very large median tooth and 1–2 small teeth on each side ; each lateral sclerite with 13 very irregular teeth. The hypopharynx unlike all *Culicoides* outside the *C. nubeculosus* group, and like the subgenus *Ceratopogon*, has its posterior border well sclerotised, and in addition, developed into three lobes bearing large teeth. *Thoracic Markings.*—Pigment absent ; paired grey translucent lateral bodies in mesothorax and metathorax.

Third Instar very similar to fourth. Head approximately 200 μ by 100 μ and 75 μ wide at oral ring.

Adults Reared 10♂♂, 14♀♀ *Stilobezzia ochracea* and 4♀♀ *S. gracilis*. Once some of these larvae were divided into two groups on head colour ; the darker headed group produced 4♂♂, 3♀♀ *S. ochracea* and the other 2♀♀ *S. gracilis* and 1♀ *S. ochracea*.

Sources of Material and Breeding Places.—Glen Clova, Angus ; Trossachs, Perthshire ; Balmaha, Stirlingshire ; Milngavie, Dumbartonshire ; Drumchapel, Lanarkshire ; Glen Urquhart, Inverness-shire ; and Strathgryfe and Bridge of Weir, Renfrewshire. Occurring on marshland in association with *Culicoides cubitalis* and *C. pallidicornis*.

Notes.—*Stilobezzia* larvae are conspicuous with dark chocolate coloured heads and white bodies, they are sluggish and never move in the typical Ceratopogonid manner, but reveal a characteristic lashing movement when picked up.

Serromyia femorata (Meigen) (Plate XVIII).

Fourth Instar.—*Head* about 180 μ by 140 μ and 70 μ wide at oral ring ; amber ; eyes relatively large. *Epipharynx* (fig. 40) with 2 combs and a narrow lateral plate on each arm ; dorsal (width 21 μ) with 7 well-separated teeth on each half ; ventral with 11 teeth. *Thoracic Markings.*—Pigment absent. Paired grey translucent lateral bodies in mesothorax and metathorax.

TABLE IV.

The percentage distribution of each species in the major larval habitats.

Species	Fresh water				Salt marsh	Dung	No. of larvae
	Bogland	Marsh	Swamp	Mud			
C. impunctatus	99	1					1,350
C. heliophilus	76	23	1				129
C. albicans	78	22					60
Isohelea spp....	96	4					474
C. truncorum...	100						635
Ceratopogon spp.	68	31		1			107
C. obsoletus	43	54	2	1			193
C. cubitalis	4	74	11	11			1,037
C. pallidicornis		95	1	4			546
C. delta	7	93					15
C. pulicaris		53	21	26	1		178
C. punctatus		60	27	13			102
C. pictipennis		100					4
C. cunctans		100					21
Stilobezzia spp.		90	4	6			228
C. vexans		100					54
C. simulator		100					1
Serromyia spp.		100					13
C. fascipennis		1	96	3			87
C. grisescens			100				3
C. odibilis		23	23	52	2		768
C. lupicaris		5	38	57			21
C. stigma		1	5	77	17		110
C. nubeculosus				93	7		30
C. circumscriptus				56	44		161
C. salinarius...					100		144
C. halophilus...					100		47
C. maritimus...					100		114
C. chiopterus...						100	281
C. pseudochiopterus						100	17
No. of sites examined ...	13	16	5	7	5	3	
No. of larvae found... ...	2,783	2,148	467	824	410	298	6,930
Percentage distribution ...	40·2	31·0	6·7	11·9	5·9	4·3	

Third Instar like fourth but head paler and 142 μ by 96 μ and 64 μ wide at oral ring.

Second Instar like third. *Head* 107 μ by 72 μ and 48 μ wide at oral ring.

Adults Reared 3♂♂, 1♀.

Sources of Material and Breeding Places.—Balmaha, Stirlingshire ; Milngavie, Dumbartonshire ; Drumchapel, Lanarkshire ; and Abbotsbury, Dorset. No adults were bred out from Dorset and it is possible that these larvae belonged to another species. *Serromyia* larvae are relatively rare members of the marshland community.

Notes.—These larvae are sluggish and never move in the characteristic Ceratopogonid manner.

LARVAL BIONOMICS.

Breeding Places of Culicoides.

The *Culicoides* larvae described in this paper were all found in very wet or waterlogged soil and it was unusual to find only one species at a time ; normally, about six species occurred, of which one or two would predominate. These breeding sites could be classified in the following manner (Table IV) : (i) Bogland, (ii) Fresh Water Marsh, (iii) Swamp, (iv) Mud, (v) Salt Marsh, (vi) Dung.

(i) The bogland breeding sites were found in the wetter areas of the moorland where the ground was covered with *Sphagnum* spp., and *Polytrichum* spp., particularly where the moss growth was penetrated by *Juncus articulatus* (*s.l.*). It is thought that the presence of the latter indicates a relatively thin layer of moss (< 6 inches) overlying the soil. Where the moss was deeper or there was surface water very few, if any, larvae were found.

These bogland habitats were dominated by *C. impunctatus* with *Ceratopogon* (*Isohelea*) spp. sub-dominant. Associated with these two were *C. truncorum, C. heliophilus, C. albicans, C. obsoletus* and *Ceratopogon* (*Ceratopogon*) spp. The last two appeared to be more catholic in their requirements and occurred equally abundantly in the next habitat.

(ii) The fresh-water marsh-breeding sites were characterised by an absence of *Sphagnum* spp. and *Polytrichum* spp. and the presence of meadow plants such as *Cardamine pratensis* and *Ranunculus* spp. In addition the water level was at, or near to, but not above the surface of the soil. On some of these sites *Juncus articulatus* (*s.l.*) was abundant and *J. conglomeratus* and *J. effusus* were often in close association, but the last two were poor " indicator " plants, since they were often found in places which became too dry in summer to support *Culicoides* larvae. The marshland sites were dominated by *C. cubitalis* with *C. pallidicornis* and *Stilobezzia* spp. sub-dominant and *C. obsoletus, C. pulicaris, C. delta, C. punctatus, C. odibilis, Ceratopogon* (*Ceratopogon*) spp. and *Serromyia* spp. in association.

(iii) In areas which are continually under water there is a change in the flora and a corresponding change in the *Culicoides* population. Thus, on the margins of a swamp covered with *Carex riparia, C. cubitalis* was dominant with *C. odibilis* sub-dominant ; but in the wetter areas of the same swamp, *C. odibilis* became dominant with *C. pulicaris* and *C. punctatus* sub-dominant.

In two other swamps, situated on the margins of lochs, the dominant *Culicoides* was *C. fascipennis.*

(iv) On areas of bare mud *C. odibilis* was dominant with *C. cubitalis, C. pallidicornis, C. pulicaris* and *C. stigma* locally abundant, but where there was slight organic pollution *C. nubeculosus* became dominant.

(v) The salt marshes varied in character from open expanses of mobile mud bearing few, if any, plants, to more settled conditions where the soil was firmly bound by vegetation. The muddy sites were dominated by *C. circumscriptus* and *C. salinarius* while the vegetated sites were dominated by *C. maritimus* with *C. halophilus* in association.

(vi) The larvae of *C. chiopterus* and *C. pseudochiopterus* have been found in old dry cakes of cow dung lying naturally in the field, and they have been encountered in this habitat in places as far apart as Rothamsted, Hertfordshire* ; and Glen Clova, Angus. In the later stages this must be one of the driest habitats occupied by *Culicoides* larvae.

Vertical Distribution of Larvae (Table II).

During the early days of larval sampling the whole of each sample was examined in separate 1 in. thick layers ; but later, in order to increase output, only the top 2 ins. were examined. The results, however, revealed specific differences in vertical distribution in the same breeding place. Thus, while the third- and fourth-instar larvae of *C. impunctatus, C. obsoletus* and *C. pallidicornis* were abundant in the top inch, those of *C. truncorum* were evenly distributed throughout the top 2 ins. *C. cubitalis* larvae were most numerous in the second inch and those of *C. heliophilus* and *C. albicans* were commonest below a depth of 2 ins. This difference in the vertical distribution of the various species may account for the existence of many species with similar requirements in the same breeding place.

The observations on *C. impunctatus* show an increasingly deeper larval distribution with age. The fact that the fourth-instar larvae are deepest suggests that the return to the surface at the onset of pupation is relatively rapid.

The significance of the sudden change in the distribution of second and third instar *C. truncorum* has already been discussed on p. 437.

Some larvae appear to be capable of climbing vertical surfaces. For example, the day after larvae of *C. salinarius, C. pulicaris* and *C. punctatus* had been placed on mud in rearing tubes, the sides of the tubes were covered with muddy trails which had obviously been left by wandering larvae. This climbing behaviour has only once been observed in daylight, and probably occurs more frequently during the night, as the larvae are negatively phototactic. All species make burrows in the rearing medium, when they can be seen against the glass ; but only in the above three species have trails been observed above the medium.

THE PUPAE.

General.

The pupae of the Ceratopogonids are light or dark brown in colour, darkest usually on the dorsum of the mesothorax, which, as in the adult, is rather humped. The integument is apparently sticky, at least when first exposed, and is often found to be covered with fine debris which may obscure some of the small features. The antennae are elongate and recurved over the eyes, their tips reaching well beyond the bases of the wings. The prothoracic respiratory organs, the " horns ", are stalked and prominent, usually projecting anteriorly and extending beyond the head ; very often at least part of the horn is heavily pigmented. The abdomen is well differentiated from the thorax and most segments have prominent ridged or spined tubercles, each usually bearing a seta. The caudal segment terminates in two conical spines. The tips of the last two pairs of legs just appear beyond the tips of the wings. The tarsi of the prothoracic legs are applied to each other along their whole length in the mid-ventral line, and the tibiae each have a notch on the mesal side near the distal end. This tibial notch appears to be characteristic of the family and may be correlated with the presence of a tibial spine in the adult.

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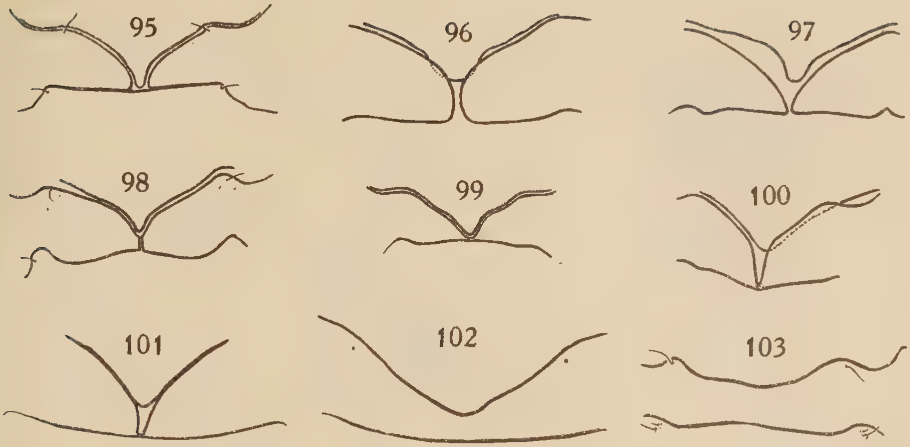
*These larvae were forwarded for identification by Mr. B. R. Laurence.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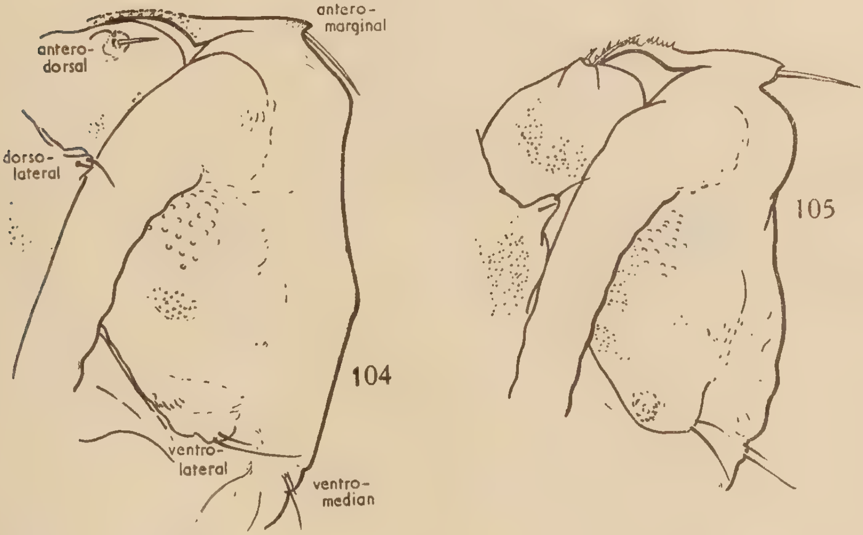

antero-marginal
antero-dorsal
dorso-lateral
104
ventro-lateral
ventro-median
105

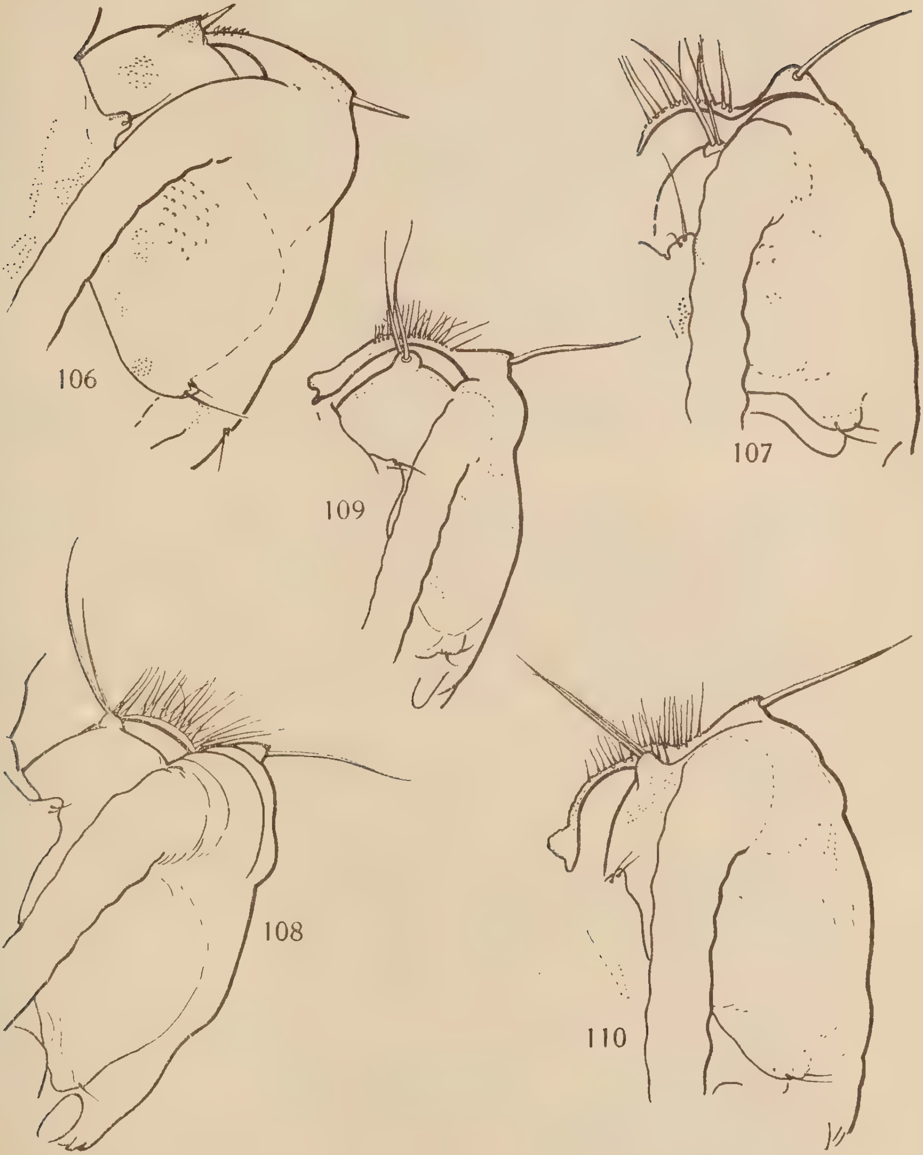
PUPAL METATHORACES

The figures show the variation in the extent and the form of the division of the metathorax in the mid-dorsal line.

Fig. 95. *C. cunctans.* Fig. 96. *C. pulicaris.* Fig. 97. *C. circumscriptus.*
Fig. 98. *C. stigma.* Fig. 99. *C. truncorum.* Fig. 100. *C. odibilis.*
Fig. 101. *Stilobezzia ochracea.* Fig. 102. *Serromyia femorata.*
Fig. 103. *Ceratopogon* (*Ceratopogon*).

LATERAL VIEW OF THE PUPAL HEAD

Fig. 104. *C. albicans.* Fig. 105. *C. salinarius.*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LATERAL VIEW OF THE PUPAL HEAD

Fig. 106. *C. odibilis.* Fig. 107. *C. obsoletus.* Fig. 108. *C. scoticus.*

Fig. 109. *C. chiopterus.* Fig. 110. *C. pseudochiopterus.*

Culicoides may be separated from the rest of the family by a number of characters. None is more than 4·5 mm. long and most are less than 3 mm. The prothoracic horns are not less than four times as long as deep, in lateral view, but are never very long and tapering as they are in some species of *Tetraphora* (= *Dasyhelea*) ; nor are they so short as in *Palpomyia* or so globular as in *Forcipomyia* ; and they are never wholly so deeply pigmented as in *Ceratopogon*. All species of *Culicoides* have the anterior margin of the metathorax deeply indented in the mid-dorsal line, with the tip of the scutellum projecting into the indentation, and the metathorax may be thus completely divided (figs. 95–100). This feature does not occur to the same extent in *Serromyia femorata* and *Ceratopogon* (figs. 102, 103). It does occur, however, in *Tetraphora* and in some species of *Stilobezzia* (fig. 101), but these forms are usually readily separated on the characters of the prothoracic horn.

Three major groups may be distinguished among *Culicoides* :—The *C. pulicaris* group, in which all the domed tracheal endings, the " papillae ", of the prothoracic horn are set closely together in a line round the tip and along the dorsal edge in the distal third (figs. 62–68). The *C. obsoletus* group (figs. 107–110), in which the cephalic setae are very long : and the *C. nubeculosus* group, in which the distal third or quarter of the horn is very deeply pigmented, while the rest is relatively pale or colourless and is marked by transverse lines or folds (figs. 43–48). The differences between the other species groups are not so striking.

Explanation of the Characters used in the Pupal Key.

The bulk of the pupal work has, of necessity, been done on the exuviae, so that some features, notably pigment spots in the abdomen, were more readily apparent than they are in the intact pupa, where the pigmentation of the integument is usually masked by the pigment of the developing adult. Nevertheless, in those species where, in the exuviae, pigment spots in the abdomen are conspicuous, they can usually also be observed in the not too mature, intact pupa by using strong transmitted light. The appearance of the prothoracic horns and of the caudal spines, the two other pigmented features used in the key, is the same in the exuviae and in the intact pupa.

Whether the exuviae or the intact pupa is used, the specimen, before being mounted, may, with advantage, be heated for a minute or so in pure lactic acid as this helps to loosen any adhering debris.

The character most used in the key, the prothoracic horn, is observed in lateral view, using a ×10 eyepiece and a $\frac{1}{6}$ in. objective. The tubercles and setae of the cephalothorax and abdomen and markings of the abdominal segments are also seen in this view. A dorsal view is needed for other characters :—The operculum ; the *dorso-median* tubercle and seta(e) (fig. 61), near the inner side of the base of the horn ; the mid-dorsal region of the metathorax ; the abdominal pigment spots (fig. 123), using a $\frac{2}{3}$ in. objective ; and the caudal spines.

Several features of the prothoracic horn are of considerable value. The pigmentation appears to be reasonably constant in degree and in extent within a species, and its variation is indicative at least of species groups. The distribution and number of papillae (the domed tracheal endings) also are characteristic of species groups ; but the variation within a species of the number of papillae appears, in some cases, to be considerable. In ten specimens of *C. halophilus*, for instance, the number of papillae varied from 11 to 18, with 14–15 as the commonest number ; Thienemann (1928) specifies *C. halophilus* as having 9 papillae. The other useful feature of the horn is the absence or presence, and the character, of the folds in its integument. In the *C. nubeculosus* group these are simple, unpigmented, transverse folds, with a tendency in some species to become dentate in the distal region. In most of the rest of the genus only these dentate projections remain as " scales ", which are usually pigmented, and may cover most of the horn.

The nomenclature used in referring to the tubercles is that proposed by Carter, Ingram & Macfie (1920). In most cases it is impracticable to define their variations, which consist in small differences in the shape and size of the tubercles and in the stoutness and pigmentation of their seta(e), but several variations are useful. In the *C. obsoletus* group the anterior cephalic tubercles—the antero-marginal (A.M.), a pair on the anterior margin of the operculum, and the antero-dorsal (A.D.), one on each side of the operculum—each have an exceedingly long seta or setae, about twice as long as those found in other species. The *lateral postero-marginal* (L.P.M.) tubercles of the abdominal segments, in the position indicated by the name, are, in most species, each prolonged into two spines, with the seta which is always present springing from the fork. In part of the *C. pulicaris* group and the *C. circumscriptus* group, however, the L.P.M. tubercles of at least the first four abdominal segments are not spined but ridged. The difference is observable only in lateral view. The *dorso-median* (D.M.) tubercles, which are additional to those named by Carter, Ingram & Macfie, are a pair situated on the prothorax, one near the base of each horn on the inner side. In all species the D.M. tubercle is not more than a slight swelling. In *C. cunctans* it bears two short, relatively stout setae : in all other species described here it bears only a single thin seta. The region of the D.M. setae is one where debris is particularly liable to collect, and it is often necessary to clear this debris away very carefully before the setae can be observed.

The markings of the abdominal segments usually take the form of pigmented spinules, dorsally, ventrally and along the anterior margin laterally, and of pale, closely-packed nodules which form a wide border to the posterior margin. In some species, such as *C. punctatus* and in *C. chiopterus*, the posterior margin of the abdominal segments has a curious mottled appearance, reminiscent of " crazy paving ", which may be described as a network of fine lines.

The operculum(=fronto-clypeus) has been figured in previous descriptions of pupae of *Culicoides* ; but, while in general it varies from group to group, the differences between those of species of the same group are small and of little taxonomic value, especially as the range of variation within a species may be considerable and the ranges of allied species may overlap ; moreover, for clear observation it must be dissected off. Consequently, in general, it is not used in the key. There is one important variation, however ; whereas in most species the operculum is more or less beset with darkly pigmented spinules, in the *C. obsoletus* group it bears many long, thin, flexible spines, which may be nearly half the length of the prothoracic horn.

In almost all species, the division of the metathorax in *Culicoides* may be regarded as being complete. In those species where the indentation does not itself extend to the posterior margin the part remaining may take one of two forms. In the first form the undivided part is usually very narrow and marked by slight extra sclerotisations : in the key a metathorax of this type is referred to as having its ends united by a thin strip. In the second form the division is completed by a sclerotised " suture ", which, in the exuviae, may be split open by too rough manipulation : a metathorax of this type is referred to in the key as having its ends abutting in a short, straight line. Where the metathorax is referred to as having its ends touching only in a point, the indentation has itself just reached the posterior margin. In *Ceratopogon* and *Serromyia femorata* the emargination or indentation does not completely divide the metathorax and is not continued to the posterior margin as extra sclerotisation or as a " suture ".

KEY TO THE PUPAE.

1. Metathorax at most indentate or emarginate on anterior border in mid-dorsal line (figs. 102, 103). Horn not more than four times as long as wide in lateral view..2

Metathorax completely divided in mid-dorsal line, or, at most, united by a short, narrow strip posteriorly (figs. 95–101). Horn at least four times as long as wide......4

2. Horn pigmented, but not opaque (fig. 75). Metathorax widely emarginate (fig. 102)......*Serromyia femorata*

Major part of horn opaquely dark (figs. 73, 74). Metathorax not at all emarginate (fig. 103)......3

3. Horn with papillae more or less regularly distributed round tip and along dorsal edge (fig. 73). No pigment spots in abdominal segments. A.M. tubercle with a long, strong seta......*Ceratopogon* (*Ceratopogon*)

Horn with about six papillae in a cluster at tip and with a cluster of smaller papillae near base, seen only with a strong light (fig. 74). Five-spot pigment pattern on the back of the abdominal segments. A.M. tubercle without a seta......*Ceratopogon* (*Isohelea*)

4. Horn pale and tapering to base and with a cluster of setae at tip (fig. 76)......*Stilobezzia ochracea*

Horn not markedly tapering to base and without setae......*Culicoides* 5

5. Some of the cephalic setae and the spines of the operculum very long, the latter at least one-quarter of the length of horn (figs. 107–110)......*C. obsoletus* Group 6

Cephalic setae not very long ; operculum with spinules (figs. 104–106)......9

6. Horn with transverse folds from one-quarter to three-quarters of the length along from base (fig. 72)......*C. pseudochiopterus*

Horn without scales or folds......7

7. Horn uniformly light brown (fig. 69)......*C. obsoletus*

Horn pigmented only in proximal third......8

8. Posterior border of fourth abdominal segment with a mottled appearance (fig. 118). The long spines of the operculum rather less than one-third of the length of A.M. setae (fig. 109)......*C. chiopterus*

Posterior border of fourth abdominal segment not mottled (fig. 117). Spines of operculum about half the length of A.M. setae (fig. 108)......*C. scoticus*

9. Horn uniformly (or nearly) brown or dark brown ; all the papillae set closely together in a line round tip and along dorsal edge in distal third (figs. 62–68)......*C. pulicaris* Group 10

Horn variously pigmented : isolated papillae proximally, often each raised on a prominence, as well as a number distally......15

10. Lateral postero-marginal (L.P.M.) tubercles of fourth abdominal segment having a spine or spines in addition to a seta......11

L.P.M. tubercles of fourth abdominal segment ridged and without spines (figs. 114, 115)......13

11. Small pupae, 2·25 mm. long. About six papillae distally in horn (fig. 68)......*C. impunctatus*

Large pupae 3·5 mm. long. More than 15 papillae in horn......12

12. Pattern of five pigment spots in abdominal segments. About 20 papillae in horn......*C. lupicaris*

No pigment spots in abdominal segments. About 17 papillae in horn. L.P.M. tubercles becoming three- to four-spined in posterior segments......*C. grisescens*

13. L.P.M. tubercles ridged and without spines in all abdominal segments......*C. pulicaris*, *C. delta*

L.P.M. tubercles becoming spined in posterior segments......14

14. In abdominal segments a network of fine lines forming a border to posterior margin (fig. 114 *C. pulicaris*). Horn with scales only (fig. 66).........*C. punctatus*
No such network in abdominal segments (fig. 115). Horn with scales dorsally and ventrally and with transverse folds laterally (fig. 67)...........*C. halophilus*

15. Horn slender and completely ringed by deep folds (fig. 60)...........*C. heliophilus*
Horn otherwise..16

16. L.P.M. tubercles of abdominal segments always with two large, dark spines between which the seta is inserted (fig. 111). Horn with black or very dark pigment distally, and sometimes also near the base ; the rest unpigmented or light brown ; with transverse folds or ridges, sometimes also with a few scales ; more than 10 papillae distally...........................*C. nubeculosus* Group 17
Pigment of the horn rarely black ; if with scales and folds then L.P.M. tubercles ridged or their spines small..21

17. Smaller pupae, 2·5 mm. long. Horn dark in distal third, otherwise unpigmented ; a few rather dark, sharp scales dorsally in third quarter, elsewhere folds ; about 13 papillae distally (fig. 47). Ends of the metathorax abutting in a short, straight line (fig. 98)..*C. stigma*
Larger pupae, over 3 mm. long..18

18. Horn dark in distal one-third, rest uniformly pale brown ; distal transverse folds becoming serrated or forming scales (figs. 46, 48)..........................19
Horn dark in distal one-third and sometimes also at base, otherwise unpigmented except round proximal papillae. Ends of metathorax rounded and touching only in a point..20

19. Tips of caudal spines dark or black. Ends of metathorax abutting in a short, straight line..*C. parroti*
Tips of caudal spines not darker than rest of the segment. Ends of metathorax rounded...*C. riethi*

20. Tips of caudal spines not darker than rest of segment.....................*C. riethi*
Tips of caudal spines dark or black.................................*C. nubeculosus*
Form A : Horn dark, though not opaque, distally (fig. 43).
Form B : Horn almost impenetrably black distally (fig. 44).
Form C : Horn darkened in a narrow region at base as well as distally (fig. 45).

21. L.P.M. tubercles large and ridged, not spined, in all segments (fig. 112).........22
L.P.M. tubercles with spines in some segments at least.............................23

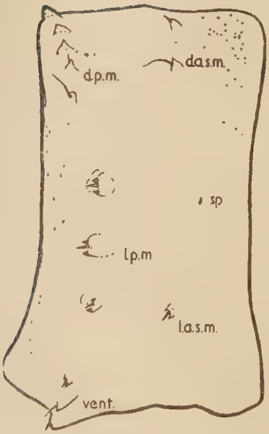
22. Very dark. Thorax densely covered with dark, irregularly shaped, small patches, fitting closely together. Horn entirely dark, becoming less dark proximally (fig. 49)..*C. vexans*
No such patches on thorax. Horn not entirely dark (figs. 55, 56)..................
C. circumscriptus,
C. salinarius

23. Dorso-median (D.M.) with two setae (fig. 61). Sensilla *v* of dorsals raised and volcano-like (fig. 121)...*C. cunctans*
D.M. with a single seta. Sensilla *v* of dorsals not raised..........................24

24. Horn uniformly light brown. Tips of the caudal spines pale........................25
Horn darkly or unevenly pigmented or both. Tips of caudal spines dark......26

25. Horn with sharp scales dorsally and ventrally and on mesal face ; none or few laterally (fig. 51)..*C. truncorum*
Horn with a few rounded scales on lateral face (fig. 54)..................*C. cubitalis*

26. L.P.M. tubercles of fourth abdominal segment ridged and without spines. Back of thorax black, with small irregular patches as in *C. vexans* ; rest of body brown with grey shading...*C. simulator*



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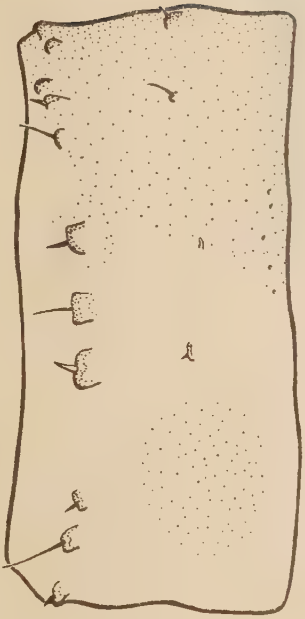

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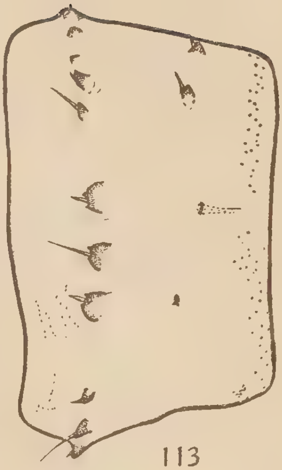

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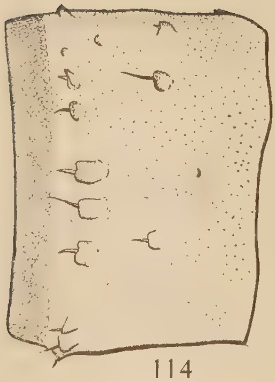

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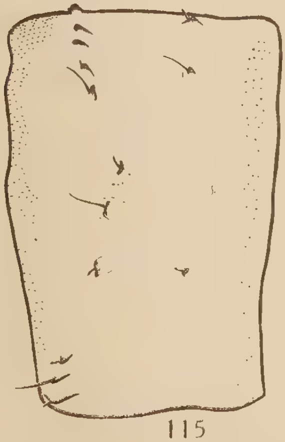

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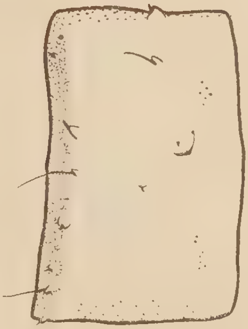

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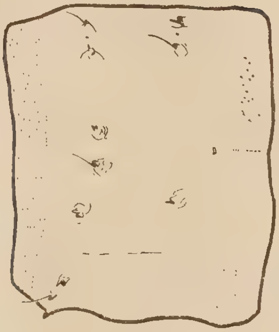
LATERAL VIEW OF THE 4th ABDOMINAL SEGMENT FROM THE RIGHT SIDE

FIG. 111. *C. stigma.* FIG. 112. *C. circumscriptus.* FIG. 113. *C. odibilis.*

FIG. 114. *C. pulicaris.* FIG. 115. *C. halophilus.* FIG. 116. *C. obsoletus.*



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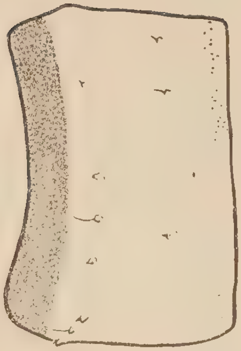

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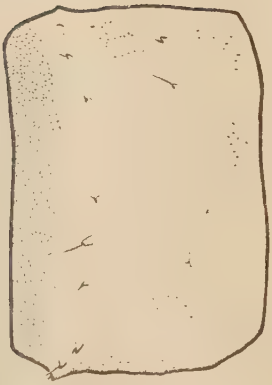

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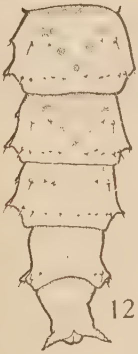

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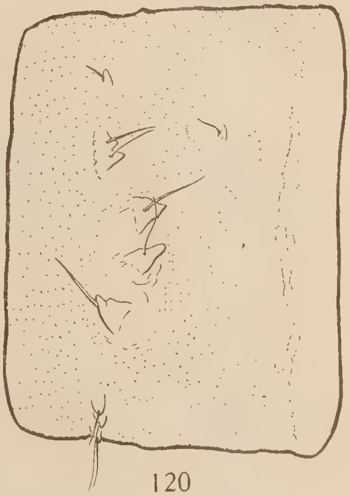

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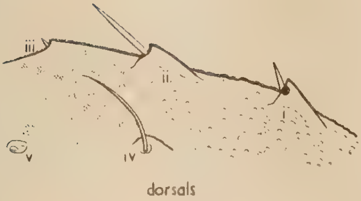

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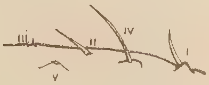

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LATERAL VIEW OF THE 4th ABDOMINAL SEGMENT FROM THE RIGHT SIDE

Fig. 117. *C. scoticus.* Fig. 118. *C. chiopterus.*

Fig. 119. *C. pseudochiopterus.* Fig. 120. *Stilobezzia ochracea.*

Fig. 121. *C. cunctans,* lateral view of the dorsal tubercles from the right side.

Fig. 122. *C. punctatus,* lateral view of the dorsal tubercles showing the mottling of the background.

Fig. 123. *C. pulicaris,* dorsal view of the posterior part of the abdomen, showing the pattern of pigment spots.

L.P.M. tubercles of fourth abdominal segment spined. Body brown or dark brown, without grey shading..27

27. Horn with three to four papillae set closely together at tip (fig. 53).................. *C. pallidicornis*
Horn with six to seven papillae at tip..28

28. Pattern of five pigment spots in each abdominal segment. Horn uniformly dark brown (fig. 52)...*C. fascipennis*
No pigment spots in abdomen. Horn unevenly pigmented........................29

29. Transverse folds as well as scales in horn (fig. 57). Intact pupa often with a greenish tinge in abdomen..*C. odibilis*
Scales, but no folds in horn...30

30. Horn deepest dorso-ventrally about middle of its length, tapering more or less regularly to each end (fig. 50). Above V.L. a tubercle armed with sclerotised ridges (fig. 104)...*C. albicans*
Horn otherwise (fig. 58). No armed tubercle above V.L., at most a few spinules on posterior region of eye..*C. maritimus*

DESCRIPTIONS OF PUPAE OF CULICOIDES.

Culicoides nubeculosus Group.

Distinguished by having the prothoracic horn deeply pigmented distally, with transverse folds in the middle region and by having the lateral postero-marginal (L.P.M.) tubercles of the fourth and subsequent abdominal segments each with two large, sharp, dark spines in addition to the normal seta which arises between them.

Culicoides nubeculosus (Meigen).

Three forms have been found, the first two corresponding to the two larval forms described on page 433.

Form A.—3·75 mm. long, brown, dark on the back of the thorax ; no pigment spots on the abdomen. *Operculum* dark and covered with relatively large spinules ; a sensilla on the lateral face of each antero-marginal (A.M.) tubercle, not immediately apparent. *Horn* (fig. 43) very dark round tip, otherwise unpigmented ; with transverse ridges or folds only, no scales : about 17 papillae round the tip and a papilla on a prominence at 1/6, 1/3 and at 2/3 of the whole length of the horn from the proximal end. *Metathorax* completely divided, the apposed ends rounded. *Antero-Marginal Tubercle* (A.M.) dark, with a dark, stout seta. *Antero-Dorsal Tubercle* (A.D.) rounded, with *a* a short, rather thin seta and *b* a stouter seta, 5/2×*a*. *Dorso-Lateral Tubercle* (D.L.) rounded, with *a* a long, thin, curved seta and *b* a darker, thin seta, 1/2×*a*. *Dorso-Median Tubercle* (D.M.) only slightly prominent, with a single, thin seta. *Ventro-Median Tubercle* (V.M.) not obvious as tubercle ; two equal, thin setae, directed posteriorly. *Ventro-Lateral Tubercle* (V.L.) rounded, with two almost equal, thin, curved setae, directed posteriorly. Dorsad of the V.L. there is a nodular prominence. *Dorsal Tubercles.* Two small, rounded tubercles, *i* and *ii*, each bearing a seta of about the same size ; posterior to these a much smaller seta *iii* : laterad of these a long, thin seta *iv*, and a sensilla *v* ; this area dark and nodular. *Fourth Abdominal Segment.*—Anterior border spinulose, posterior border nodular. *Lateral Postero-Marginal Tubercles* (L.P.M.). All three tubercles in each of the fourth and subsequent segments with two, sharp, dark spines, between which the normal seta arises. *Caudal Spines* directed at about 60° to the long axis ; tips dark.

Form B.—4·00 mm. long. A pattern of 5 pigment spots on the dorsum of each abdominal segment (fig. 123) like that described for *C. nubeculosus* by Mayer (1934). *Operculum* with an obvious sensilla immediately behind each A.M. tubercle. *Horn* (fig. 44) almost impenetrably black round the tip ; unpigmented elsewhere, except very slightly on the proximal prominences : with transverse folds. About 20 papillae round the tip, very difficult to see because of the density of the pigment. A papilla on a prominence at 1/8 and at 1/4 ; occasionally two papillae in the region of 1/8.

Form C.—Close to Form A, except that the respiratory horn (fig. 45) has a ring of black pigment round the base, in addition to the distal pigment. Ayrshire, in coll. British Museum (Natural History), coll. F. W. Edwards.

Culicoides riethi Kieffer.

3·5 mm. long. Dark, with a 5–spot pattern on the abdominal segments. *Operculum* (fig. 77) covered with small spinules. *Horn* (fig. 46) dark at the tip and a slight darkening at the base, otherwise unpigmented ; with transverse folds tending to form spines in the distal region. About 19 papillae round the tip ; 3 papillae on slightly darkened prominences in the proximal half. *Metathorax* completely divided ; the apposed ends rounded. *V.L.* a single, rather short and stout straight seta. *Caudal Spines.*—Tips not darker than rest of segment.

Culicoides stigma (Meigen).

2·5 mm. long. Dark on the back of thorax anteriorly, paler posteriorly. Abdomen pale ; two faint dorsal pigment spots on each of segments 1–7, apparent only in exuviae. *Operculum* (fig. 78) dark and closely covered with dark, sharp spinules. A sensilla on the posterior side of the base of each A.M. tubercle. *Horn* (fig. 47). Distal 1/3 very dark almost black ; rest pale. A few rather dark, sharp spines (scales) in the third quarter, otherwise continuous transverse folds. Thirteen papillae visible at the tip in lateral view, though possibly more are present, obscured by the density of the pigment ; a papilla on a prominence at 1/6 and at 1/3, or a single papilla on a prominence at 1/4. *Metathorax* (fig. 98) completely divided, the ends apposed in a short, straight line posteriorly. *Fourth Abdominal Segment* (fig. 111). A very few spinules on anterior border ; pale nodules on posterior border. *Caudal Spines* directed posteriorly at rather less than 45° to the long axis ; tips very dark brown or black.

Culicoides parroti Kieffer.

Manchester ; British Museum (Natural History) collections. 3·5 mm. long. Dark on back of thorax. Dorsally a 5-spot pigment pattern on each abdominal segment, probably seen only in exuviae. *Operculum* (fig. 79) very spinulose, the spinules dark and large laterally. *Horn* (fig. 48) very dark, almost black in distal 1/3 ; rest uniformly light brown. Folds becoming serrated or dentate distally. Sixteen papillae round tip ; a papilla on each of two slight tubercles in proximal 1/4. *Metathorax* completely divided, the ends abutting in a short, straight line posteriorly. *Fourth Abdominal Segment* nodular posteriorly and anteriorly, dorsally and ventrally, but not laterally. *Caudal Spines* directed at 45° ; tips very dark or black.

Culicoides vexans (Staeger).

3·25–3·5 mm. long. Very dark all over. Thorax densely covered with small, dark, irregularly shaped patches or nodules, fitting closely together. Faint pigment pattern on abdominal segments, obscured by the dense covering of spinules. *Operculum* dark and irregularly covered with dark spinules. *Horn* (fig. 49) entirely dark, darkest at tip, becoming progressively less dark towards base. A few folds laterally, becoming large rounded scales distally ; scales dorsally and ventrally. Seven papillae at tip ; one at 3/4 and 4 in the proximal 1/2. *Metathorax.*—The ends abutting in a short, straight line. *Dorsals.*—Setae *i* and *ii* about equal, both dark and stout. *Fourth Abdominal Segment* dark ; very spinulose dorsally, less so laterally ; very nodular posteriorly. *L.P.M.* large, dark and ridged, not spined, in segments 4–7. *Caudal Spines* dark tipped.

Culicoides albicans (Winnertz).

3 mm. long. Very dark on back of thorax. No pigment spots on abdominal segments. *Operculum* (fig. 80) covered with spinules and nodules, except posteriorly. Two irregular rows of larger spinules on each lateral margin. More nodular anteriorly. *Horn* (fig. 50) dark brown, except for a small, proximal light patch ; tip slightly darker than rest. In shape deepest dorso-ventrally in proximal 1/2, tapering slightly towards tip. A few dark scales in middle region. Seven papillae round tip ; three equidistant in proximal 1/2. *Metathorax.*—The ends apposed in a short, straight line. *V.L.*—Two thin, sub-equal setae. Dorsad of these (fig. 104) a prominent tubercle with sclerotised " contour " ridges. *Fourth Abdominal Segment.*—Broad anterior border of spinules ; dorsally and scattered elsewhere, except posteriorly. Broad posterior border of nodules. *L.P.M.*—Two-spined, the spines short and rounded. *Caudal Spines* directed posteriorly ; tips dark.

Culicoides truncorum Edwards.

2 mm. long. Pale, especially in abdomen. *Operculum* (fig. 81). Only a few marginal spinules anteriorly ; bare elsewhere, or with a few striations posteriorly. *Horn* (fig. 51) uniformly pale brown, except at extreme tip and base, where it is quite pale. Five or six papillae round tip and 2 in proximal 3/4. With a few dark scales, usually on mesal face only. *Metathorax* (fig. 99) not quite divided, the ends united by a very thin strip. In one specimen (♂) completely divided, the ends separated by the scutellum. *V.L.*—Dorsad of the V.L. tubercle occasionally a small, nodular tubercle. *Dorsals.*—Seta $i = 2 \times ii$; both dark. *Fourth Abdominal Segment.* Anterior and posterior borders with a few nodules dorsally and ventrally. *L.P.M.*—In the fourth abdominal segment each tubercle with one or two small, sharp spines ; with two spines each in the posterior segments. *Caudal Spines* variable ; may be dark or pale.

Culicoides fascipennis (Staeger).

2·5–2·75 mm. long. Blackish brown ; very dark on back of thorax. Pigment spots on abdominal segments. *Operculum* dark. Double row of spinules laterally, not reaching posterior end ; spinules anteriorly and centrally, not posteriorly; oblique striations posteriorly. *Horn* (fig. 52) dark brown ; darkest near tip, paler near base. Dark scales dorsally and ventrally ; overlapping or imbricated on mesal face ; on lateral face usually only a few scales, occasionally with a few transverse folds. Nine papillae at tip ; 2–4 on slight prominences in proximal 3/4. *Metathorax.*—The ends drawn out sharply and abutting in a very short, straight line. *A.M.* with a definite spine projecting above the dark, stout seta. Dorsal to the V.L. tubercle a conical tubercle armed with a few sclerotised ridges. *Dorsals.*—Setae *i* and *ii* about equal. *Fourth Abdominal Segment.*—Spinules anteriorly, pale nodules posteriorly. *L.P.M.*—Each of the tubercles in the fourth–eighth abdominal segments with two small, sharp spines. *Caudal Spines* dark tipped.

Culicoides pallidicornis Kieffer.

2·1 mm. long. Abdomen pale ; darker on back of thorax. *Operculum* (fig. 82). Row of spinules anteriorly on each side, decreasing in size posteriorly. Irregular double row centrally. *Horn* (fig. 53) darkest distally, becoming paler proximally ; distal 2/3 dark. Black tipped scales. Group of 3 papillae at tip and a single one near them ; 1 at 1/4, at 1/2 and at 2/3. *Metathorax.*—The ends united by a long, narrow strip. *A.M.* with a spine above the long, dark seta. *Dorsals.*—Setae *i* and *ii* about equal. *Fourth Abdominal Segment.*—Anterior border spinulose, posterior border nodular. *L.P.M.*—Each tubercle in the fourth–eighth abdominal segments with two spines. *Caudal Spines* dark tipped.

Culicoides cubitalis Edwards.

2 mm. long. Pale brown. *Operculum* (fig. 83).—On each side a row of about 6 transverse ridges, followed by about 3 large and then about 3 small spinules. Posteriorly a few striations (atypical in fig. 83). *Horn* (fig. 54) uniformly pale brown ; a few scales with dark tips. About 5 papillae distally ; 1 at 1/6, 1/4, 2/5 and 3/5. *Metathorax.*—The ends united by a long, narrow strip. *A.M.*—The seta long, stout and pale. *Dorsals.*—Seta *i* about $3/2 \times ii$, and about equal to *iii*. *Fourth Abdominal Segment.*—Anterior border spinulose ; posterior border nodular. *L.P.M.*—Each tubercle in the fourth-eighth abdominal segments with two small spines. *Caudal Spines.*—Tips not darker than rest of segment.

Culicoides pictipennis (Staeger).

General Appearance.—3·00 mm. long. Dark brown, without pigment spots on abdomen ; the back of the thorax blotched and nodular. *Operculum.*—Dark ; a row of dark, thick spinules on each lateral margin, the rest irregularly spinulose, with some striations posteriorly. *Horn* (fig. 54*a*).—Uniformly dark brown, except for a very narrow pale area at base. The middle third with rather round-tipped scales, hardly darker than the background. About 8 papillae round tip ; a papilla at 2/3, at 1/3 and two in the proximal 1/6. *Metathorax.*—Completely divided, the ends abutting. *A.M.*—The tubercle with a prominent spine above the long, dark seta. *Dorsals* $i = 2/3 \times ii$. *L.P.M.*—The tubercles ridged, not spined, in all segments ; the ridge rather short, the tubercle appearing truncated. *Caudal Spines* black tipped.

Note.—This species is not given in the key to the pupae. It runs down, however, to the *C. circumscriptus*–*C. salinarius* group, from which species it may be separated by the absence of transverse folds or ridges from its prothoracic horn.

Culicoides circumscriptus Kieffer, **Culicoides salinarius** Kieffer.

The pupae of these two species form a slightly heterogeneous group, the heterogeneity of which appears not to depend on the species or on the locality, so far as this has been investigated. The specimens of *C. salinarius* examined were taken at Beauly, Inverness-shire, and at Hayling Island, Hants (the latter taken by Mr. J. Staley and lent by the British Museum) ; those of *C. circumscriptus* were taken at Charmouth, Dorset, and by Mr. R. Hartland-Rowe at Dawlish, S. Devon. In each of these groups the principal characters showed small individual variations, corresponding with similar variations in one or more of the other groups. The extreme forms of some of the variant characters appeared among specimens from the same locality, as well as in those from different localities. In consequence, the two species were indistinguishable, even as geographical races.

As a group *C. circumscriptus* and *C. salinarius* are distinguished by having the distal quarter of the horn dark, while at least most of the rest is pale brown ; and by having the L.P.M. tubercles large, ridged and without spines in all except the most anterior abdominal segments.

Length, 2·5–3·5 mm. dark, especially on back of thorax. Dorsally, on each abdominal segment, a 5-spot pigment pattern, which may be dark and clearly defined or faint. *Operculum* (figs. 84, 85) dark and irregularly spinulose, the spinules larger laterally. *Horn* (figs. 55, 56) brown to very dark in distal 1/5–1/4 ; rest pale brown, occasionally with more or less extra darkening in proximal 1/4, with or without extra darkening along dorsal edge. Often with sharp scales along dorsal and sometimes ventral edge ; mesal and lateral faces at least with transverse folds ; mesal face often with scaly folds and sharp scales distally ; lateral face less often with scaly folds or scales distally. Eight to thirteen papillae at the tip and 2–5 on slightly darkened prominences in the proximal 1/2–3/4. *Metathorax* (fig. 97) completely divided and usually slightly separated, the ends roughly triangular in appearance.

V.L. dorsal to the V.L. tubercle a small, but prominent and usually conspicuous tubercle armed with triangular spines or ridges (fig. 105) : this armed tubercle was absent in one specimen of *C. circumscriptus* from Charmouth. The posterior aspect of the eye, near this tubercle, is very spiny. *Dorsals.*—Seta *i* usually slightly longer than *ii*. *Fourth Abdominal Segment* (fig. 112). Anterior border spinulose dorsally and ventrally, with or without nodules laterally ; occasionally with spinules round the bases of the L.P.M. tubercles on the posterior side. Posterior border nodular. *L.P.M.* large, ridged and without spines in the fourth–eighth abdominal segments. *Caudal Spines.*—Tips dark brown or black.

Culicoides odibilis Austen.

2·5 mm. long. Dark on back of thorax ; in the mature pupa very often a greenish tinge, especially in the abdomen. *Operculum* (fig. 86) covered with small, dark spinules, smaller posteriorly and centrally, larger anteriorly and laterally. *Horn* (fig. 57) usually entirely pigmented brown, with extra darkening in the distal 1/4 ; occasionally, general darkening may be slight and extra darkening may be absent. Folds and triangular, dark scales in proximal 2/3. Six or seven papillae distally ; 2–3 in proximal 1/4 and 1 at 1/2–2/3. *Metathorax* (fig. 100) deeply cleft, but usually not completely divided ; the ends united by a narrow strip. *V.L.*—Dorsal to the V.L. tubercle a small, but prominent tubercle armed with triangular spines (fig. 106). *Dorsals.*—Seta *i* slightly longer than *ii*. *Fourth Abdominal Segment* (fig. 113). A faint anterior, median, dorsal pigment spot. Spinules on anterior border ; nodules on posterior border. *L.P.M.*—Tubercles large, each with two small, sharp spines, not becoming larger in the posterior segments. *Caudal Spines.*—Tips black.

Culicoides maritimus Kieffer.

2·5 mm. long. Dark on back of thorax. *Operculum* (fig. 87) with rather long, dark spinules laterally ; none posteriorly ; many anteriorly. *Horn* (fig. 58) dark, except for a small proximal area ; darkest distally, becoming less dark proximally. A few scattered, triangular scales in the proximal 2/3. About 7 large, clear papillae at tip ; 2 in proximal 1/3. *Metathorax* completely divided ; the ends rounded and a little separated. *V.L.*—No armed tubercle dorsal to the V.L., but a few triangular spinules on posterior aspect of eye. *Dorsals.*—Setae *i* and *ii* short, stout and equal. *Fourth Abdominal Segment.*—Spinules dorsally on anterior border ; nodules on posterior border. *L.P.M.* each with two small spines in fourth–eighth abdominal segments. *Caudal Spines.*—Tips very dark or black.

Culicoides simulator Edwards.

3·0 mm. long. Black on back of thorax, with small, dark, irregular spots, similar to those of *C. vexans*. Rest of body appears brown, with dark grey shading, except round anterior margin and behind posterior tubercles in each segment. No pigment spots in abdomen. *Operculum* very dark and densely spinulose. *Horn* (fig. 59) entirely dark, distal 1/5 darkest, rest uniformly dark. Scales dorsally, only a few scales laterally. About 6 papillae at tip ; 3 equidistant on slight prominences in proximal 2/3. *Metathorax* completely divided. *V.L.*—A spined tubercle dorsal to the V.L. *Dorsals.*—Setae *i* and *ii* stout, dark and equal. *Fourth Abdominal Segment.*—Anterior margin browner than rest. Spinulose dorsally and ventrally ; nodular posteriorly. *L.P.M.*—In fourth abdominal segment ridged, not spined ; becoming spined in posterior segments. *Caudal Spines.*—Tips black.

Culicoides heliophilus Edwards.

2·0–2·5 mm. long. Pale brown ; dark on back of thorax. *Operculum* (fig. 88) lightly pigmented, with a few spinules anteriorly or transverse ridges ; single row of spinules on each side. *Horn* (fig. 60) transparent blackish brown in distal 1/4–1/3, rest pale brown, with, occasionally, a slight extra darkening in proximal 1/3. Without scales, but with deep, transverse, encircling folds. Group of 5–6 papillae at tip; 2–3 on slightly darkened prominences in proximal 2/3–3/4. *Metathorax* completely divided and slightly separated. *V.L.*—Dorsal to V.L. often a small, spined or ridged tubercle or a few ridges in its place. *Dorsals.*—Setae *i* and *ii* short, stout and equal. *Fourth Abdominal Segment.*—Spinules dorsally and ventrally on anterior border; nodules on posterior border. *L.P.M.* each with two slightly rounded spines in fourth–eighth abdominal segments. *Caudal Spines.*—Tips black.

Culicoides cunctans (Winnertz).

2·25 mm. long. Pale brown. *Operculum* (fig. 89) dark, nodules anteriorly in centre; spinules along lateral borders; striations postero-laterally. *Horn* (fig. 61) uniformly brown, except for a slightly paler area at base and at extreme tip. A few scales, hardly darker than rest of horn, dorsally and ventrally, but not laterally. About 7 papillae at tip; 1 at 1/3 and at 2/3. *Metathorax* completely divided, with the ends apposed in a short, straight line. *D.M.* (fig. 61).—Two setae: inner rather stout and outer, nearer horn, slightly longer and thinner. *Dorsals* (fig. 121).—Setae *i* and *ii* stout, dark and equal; seta *iv* nearly twice as long and equally stout; sensilla *v* raised and volcano-like. *Fourth Abdominal Segment* not at all spinulose or nodular; a very few pale spinules occur in the caudal segment. *L.P.M.* pale, ridged and without spines in fourth abdominal segment; with a tendency to acquire one or two small spines in at least one of the subsequent segments. *Caudal Spines.*—Tips not darker than rest of segment.

Culicoides pulicaris Group.

Pupae of this group are distinguished by having all the papillae of the horn set closely together in a line round the tip and along the dorsal edge and none at all in the proximal region. In most cases the horn itself, in lateral view, has its sides nearly parallel, and is about 1/4 as wide as it is long.

Culicoides lupicaris Downes & Kettle.

3·5 mm. long. Very dark, with conspicuous 5-spot pigment pattern in each abdominal segment. *Operculum* (fig. 90) very dark and densely covered with mostly blunt spinules. Large nodular prominence posteriorly. *Horn* (fig. 62) all dark; very dark round tip, not quite so dark in proximal 1/4 and least dark in middle region. Proximal 2/3 closely covered with dark, sharp scales. Irregular line of about 21 papillae distally. *Metathorax* completely divided, the ends slightly separated. *Dorsals.*—Tubercles small and sharp-pointed; the setae short and stout, *i*=3/4×*ii*. *Fourth Abdominal Segment* entirely nodular, except anteriorly, where it is spinulose, and posteriorly, where it has a border composed of a network of fine lines. *L.P.M.* all with a single spine. *Caudal Spines.*—Tips dark.

Culicoides grisescens Edwards.

3·5 mm. long. Back of thorax dark, with a slightly mottled appearance; rest light brown. *Operculum* not especially dark. Row of dark spinules on each side, not reaching posterior end; spinulose anteriorly; posteriorly a ridged tubercle. *Horn* (fig. 63) uniformly light brown, except for very narrow paler basal region. Sharp, rather dark scales laterally, mesally and dorsally and ventrally. About 17 papillae in a line reaching halfway along from distal end, the proximal 8 or so tending to run along mesal side of dorsal edge. *Metathorax* completely divided, the ends rather broadly rounded. *Dorsals.*—Seta *i* stouter than, but only 2/3 the length of *ii*. *Fourth Abdominal Segment.*—Rather pale sharp spinules, linked in lines by thin ridges, on anterior margin. A reticulate appearance on rest of segment and with a close network of fine lines on posterior margin resembling " crazy paving " (1/6 objective). *L.P.M.* each with two small, sharp spines in fourth abdominal segment, becoming slightly larger and increasing in number to 3–4 on each tubercle in subsequent segments. *Caudal Spines.*—Tips black.

Culicoides delta Edwards.

3·0 mm. long. Pale except for back of thorax. Pattern of pigment spots in abdominal segments, evident at least in exuviae. *Operculum* (fig. 91). Larger conical spinules anteriorly, smaller posteriorly. *Horn* (fig. 64) uniformly brown or nearly so, except for slightly paler areas at tip and at base. Regular, sharp-tipped scales in proximal half. About 16 papillae in line reaching back from tip to a little beyond distal 1/3. *Metathorax* not quite completely divided, the narrow, uniting strip sclerotised. *Dorsals.*—Seta *i* slightly shorter and thinner than *ii*. *Fourth Abdominal Segment* spinulose anteriorly ; posterior border with a network of fine lines (" crazy paving "). *L.P.M.* all ridged and without spines. *Caudal Spines.*—Tips brown, not darker than rest of segment.

Culicoides pulicaris (L.).

3·5 mm. long. Very dark on back of thorax, but without a mottled appearance. Pattern of pigment spots on the abdominal segments (fig. 123). *Operculum* (fig. 92) deeply cleft between A.M. tubercles. Dark, irregularly covered with spinules. At posterior end an inverted V, formed by sclerotised striations, filled with spinules. *Horn* (fig. 65) uniformly light brown except for small, paler area at base. A few scales in middle 1/3. Fifteen to seventeen papillae in a line distally. *Metathorax* (fig. 96) completely divided, the ends rounded. *Dorsals.*—Well-marked spine on each tubercle ; seta *i* slightly shorter and stouter than *ii*. *Fourth Abdominal Segment* (fig. 114). Anterior border spinulose ; posterior border with broad margin formed by network of fine lines. *L.P.M.* all large, ridged and without spines. *Caudal Spines.*—Tips dark.

Culicoides punctatus (Meigen).

3·5 mm. long. Generally darker than *C. pulicaris*. Mottled appearance on back of thorax (fig. 122). Pattern of pigment spots on abdominal segments, sometimes very faint. *Operculum* (fig. 93). Posterior edges bordered with dark spinules. Inverted V posteriorly, filled with spinules. Anterior region densely and irregularly covered with spinules. Occasionally the inverted V is represented by a spiny tubercle. *Horn* (fig. 66) entirely dark, except for narrow pale region at base ; darkest just short of tip, or uniformly dark. Rather dark, very sharp scales in 2/3–3/4 on lateral face, many more such on mesal face ; rather more scaly than *C. pulicaris*. Eleven to sixteen papillae in a line distally. *Metathorax* not quite completely divided, the narrow uniting strip sclerotised ; or completely divided, the ends sclerotised and abutting in a short, straight line. *Dorsals* (fig. 122).—Seta *i* only half as long as *ii*. *Fourth Abdominal Segment.*—Spinulose anteriorly ; posterior border nodular and with a network of fine lines. *L.P.M.* all ridged and without spines in fourth abdominal segment ; becoming spined in posterior segments. *Caudal Spines.*—Tips dark.

Culicoides halophilus Kieffer.

2·75 mm. long. Back of thorax very dark and mottled as in *C. punctatus*. *Operculum* (fig. 94) very variable ; may be simply irregularly spinulose ; the posterior region may be relatively free from spinules ; there may be a row of rather large spinules along each side ; and there may be a median posterior inverted V, which may or may not be filled with spinules. *Horn* (fig. 67) uniformly dark brown ; on lateral face transverse folds in proximal 1/3–1/2 ; scales on dorsal and ventral edges and on mesal face. Line of 11–18 papillae distally, with 14–15 as commonest number. Thienemann (1928) specifies *C. halophilus* as having 9 papillae. *Metathorax* completely divided, the rounded ends slightly separated. *Dorsals.*—

Tubercles sharp-pointed or spined ; seta *i* slightly less than *ii*. *Fourth Abdominal Segment* (fig. 115). Anterior border spinulose ; posterior border nodular and without a network of fine lines. *L.P.M.* all ridged and without spines. *Caudal Spines.*—Tips dark.

Culicoides impunctatus Goetghebuer.

2·2 mm. long. Brown. *Operculum* covered with dark spinules. *Horn* (fig. 68) uniformly dark brown, except at tip and base ; a few scales in proximal 1/2. Six papillae distally. *Metathorax* not completely divided, the narrow uniting strip sclerotised. *Dorsals.*—Seta *i* slightly less than *ii*. *Fourth Abdominal Segment.*—Anterior border spinulose. *L.P.M.*—Tubercles without spines. *Caudal Spines.*—Tips black.

Culicoides obsoletus Group.

Pupae of this group are clearly distinguished by the great length of the cephalic setae and the opercular " spinules ", which may be 1/4–1/2 the length of the horn.

Culicoides obsoletus (Meigen).

2·5 mm. long. Pale brown. Cephalic setae very evident (fig. 107). *Operculum* covered with very long " spinules ", about half the length of horn. *Horn* (fig. 69) uniformly light brown ; no scales, no folds or ridges. About 6 papillae at tip and 3–4 in proximal 3/4. *Metathorax* completely divided, tip of scutellum separating the ends. *V.M.*—Absent. *Dorsals.*—Seta *i* stouter than and about 1/3 of *ii*. *Fourth Abdominal Segment* (fig. 116). Nodular dorsally and ventrally ; a few spinules anteriorly and posteriorly ; posterior border with network of fine lines. Only one D.P.S.M. tubercle and seta, with one seta base dorsal to it. *L.P.M.*—Tubercles conical. *Caudal Spines.*—Tips only slightly darkened.

Culicoides scoticus Downes & Kettle.

2·5 mm. long. Pale brown, with elongate appearance. Thorax not at all spinulose. *Operculum* covered with very long, thin spines. *Horn* (fig. 70) slightly darkened in proximal 1/3 ; a narrow pale region at base ; without scales or folds. Five papillae at tip ; 4–5 in proximal 3/4. *Metathorax* completely divided, the ends rather pointed and appreciably separated, tip of scutellum between them. *A.M.* (fig. 108). Small tubercle with very long seta, more than twice as long as the spines of the operculum. *V.M.*—Single very small seta. *V.L.*—Single thin seta. *Dorsals.*—Tubercles sharp-pointed ; seta $i = 1/3 \times ii$. *Fourth Abdominal Segment* (fig. 117). Anterior border spinulose dorsally and ventrally ; nodular posteriorly. *L.P.M.*—Tubercles conical, *i.e.*, having a single blunt spine. *Caudal Spines.*—Tips brown.

Culicoides chiopterus (Meigen).

2·0 mm. long. Pale. Long cephalic setae. *Operculum* covered with long spines, not so long as those of *C. scoticus*, slightly less than 1/3 of the length of the setae of the A.M. (fig. 109). A nodule at posterior end. *Horn* (fig. 71) pale, except for a dark patch in proximal 1/3, mainly on ventral side. Without scales or folds. Five papillae at tip ; 5 distributed more or less regularly along dorsal edge. *Metathorax* indented slightly on posterior edge as well as anteriorly ; the ends drawn out and united by only a thin strip. *A.M.*—Seta very long. *V.M.*—Absent. *Dorsals.*—Seta *i* short and conical, only $1/5 \times ii$. *Fourth Abdominal Segment* (fig. 118). A few spinules anteriorly ; posterior border mottled. Only one D.P.S.M. tubercle in each segment. *L.P.M.*—Tubercles with a single spine. *Caudal Spines.*—Tips dark.

Culicoides pseudochiopterus Downes & Kettle.

2·5 mm. long. Pale brown. Cephalic setae evident (fig. 110). *Operculum* covered with long spines, not so long as those of *C. scoticus*, rather less than 1/3 of setae of A.M. nodule at posterior end. *Horn* (fig. 72) very slightly darkened in proximal 1/6, otherwise almost unpigmented. Deep folds from 1/4–3/4. Five or six papillae at tip ; 2 in proximal 1/6 ; 1 at 1/3. *Metathorax.*—The ends drawn out almost to a point and well separated. *A.M.*—Seta very long, more than three times as long as opercular spines. *V.M.*—Absent. *Dorsals.*—Seta $i=1/2\times ii$. *Fourth Abdominal Segment* (fig. 119) pale, but very rugose (1/6 objective) ; posterior border with pale nodules, rather like an incomplete network of fine lines ; a few spinules anteriorly. *L.P.M.*—Tubercles conical. *Caudal Spines.*—Tips hardly darker than rest of segment.

DESCRIPTIONS OF PUPAE OF OTHER GENERA.

Ceratopogon (**Ceratopogon**) sp.

3·0 mm. long. Amber-coloured ; back of thorax dark and nodular. No pattern of pigment spots in abdominal segments. *Operculum* covered more or less regularly with small, dark nodules, fewer posteriorly than anteriorly. *Horn* (fig. 73) short, deep (less than four times as long as wide in lateral view). Opaquely black, except round tip and along dorsal edge, where it is translucent, but dark. About 15 papillae distributed more or less regularly round tip and along dorsal edge. *Metathorax* (fig. 103) not at all indentate. *A.D.*—A single short seta. *Dorsals.*—Very small tubercles. Seta $i=1/2-2/3\times ii=iii$. *Fourth Abdominal Segment.*—Transparent nodules dorsally, ventrally and posteriorly. *L.P.M.*—Tubercles small and rounded. *Caudal Spines* short and not darker than rest of segment.

Ceratopogon (**Isohelea**) sp.

Less than 2·0 mm. long. Pale brown, except for back of thorax, which is dark, owing to the presence of dark nodules. Pattern of 5 pigment spots in each abdominal segment. *Operculum* dark and covered anteriorly with dark nodules ; a border of dark spinules laterally, reaching to posterior end ; central posterior region fairly clear. *Horn* (fig. 74) short and deep (nearly four times as long as wide in lateral view). Very dark and surface rugged. Relatively clear at extreme tip, showing a fan of about 6 papillae ; on dorsal edge, near base, a number of small papillae, seen only with an amber filter and strong light. *Metathorax* not at all indentate. *A.M.*—Flattened tubercle without a seta. *A.D.*—A single, very short, stout seta. *V.M.*—A small tubercle without a seta. *Dorsals.*—No tubercles ; setae *i* and *ii* both very short. *Fourth Abdominal Segment.*—A few spinules dorsally, ventrally and laterally. Only two D.P.M. tubercles. *L.P.M.*—Small tubercles, not spined. Second tubercle displaced anteriorly. *Caudal Spines.*—Not darker than rest of segment.

Serromyia femorata (Meigen).

3·5 mm. long. Pale. *Operculum* closely covered with nodules, background pale. *Horn* (fig. 75) short, about four times as long as broad in lateral view. Dark, except at base where it is pale. No scales. Eight or nine papillae on prominences round tip and distal 1/3. *Metathorax* (fig. 102) widely indentate (emarginate), but not divided. *A.M.*—Small, rugose tubercle with a short seta. *A.D.*—Low, rounded tubercle with a single short seta. *D.L.*—Two very small spines. *V.M.*—Absent. *Dorsals.*—Setae *i* and *ii* both on the same rounded tubercle ; seta *iv* posterior to sensilla *v*—the opposite of their relative positions in *Culicoides*. Seta *i* slightly greater than *ii*. *Fourth Abdominal Segment.*—Posterior border with pale nodules ; anterior border with nodules and a few spinules. *L.P.M.*—Two rounded tubercles on the same prominence ; one with 3 very short setae, and the other with a single very short seta. This is quite unlike the arrangement in *Culicoides*. *Caudal Spines* directed at 60° to long axis ; tips dark.

Stilobezzia ochracea (Winnertz).

3·0 mm. long. Pale amber ; back of thorax with a few unpigmented nodules and not darkened. *Operculum* pale amber, with a few nodules not more pigmented than background. *Horn* (fig. 76) elongate and club-shaped, without scales or folds ; with a cluster of short setae at tip ; a fan of about 8 papillae at tip. *Metathorax* (fig. 101) completely divided. *A.M.*—Low tubercle with a long, thin seta. *A.D.*—Very small tubercle with a long, thin seta and a sensilla. *D.L.*—Three setae ; one long and thin ; a second short and thin ; and a third short and peg-like. *D.M.*—Two almost equal setae, lying much nearer the D.L. than in *Culicoides*. *Dorsals.*—No tubercles : three nearly equal, long, thin setae. *Fourth Abdominal Segment* (fig. 120).—A narrow anterior border of spinules linked by sclerotised ridges. Posterior border of nodules. *L.P.M.*—Tubercles large and conical, arising from the same prominence. *Caudal Spines* directed at 45° to long axis ; not darker than rest of segment.

Summary.

This paper presents a key to the larvae and pupae of 28 species of *Culicoides* found in Britain and to larvae and pupae of the genera *Stilobezzia*, *Serromyia* and *Ceratopogon* including the subgenera *Ceratopogon* and *Isohelea*. The keys are supplemented by descriptions of the larvae and pupae, including photographs of the fourth instars and figures of the so-called " hypopharynx "—the true epipharynx—of most of the larvae and by figures of specific characters of the pupae. Twenty-eight species of *Culicoides* larvae are described :—*C. albicans*, *C. chiopterus*, *C. circumscriptus*, *C. cubitalis*, *C. cunctans*, *C. delta*, *C. fascipennis*, *C. grisescens*, *C. halophilus*, *C. heliophilus*, *C. impunctatus*, *C. lupicaris*, *C. maritimus*, *C. nubeculosus*, *C. obsoletus*, *C. odibilis*, *C. pallidicornis*, *C. pictipennis*, *C. pseudochiopterus*, *C. pulicaris*, *C. punctatus*, *C. riethi*, *C. salinarius*, *C. scoticus*, *C. simulator*, *C. stigma*, *C. truncorum*, and *C. vexans*. The descriptions of the pupae include all the above, with the addition of *C. parroti*.

An analysis has been made of the breeding preferences of *Culicoides* and it was found that species could be placed in one of six groups depending on the larval habitat. The six categories were :—(i) Bog, (ii) Fresh Water Marsh, (iii) Swamp, (iv) Mud, (v) Salt Water Marsh and (vi) Dung.

The vertical distributions of seven species of *Culicoides* larvae are given. There are marked differences between the species in this respect.

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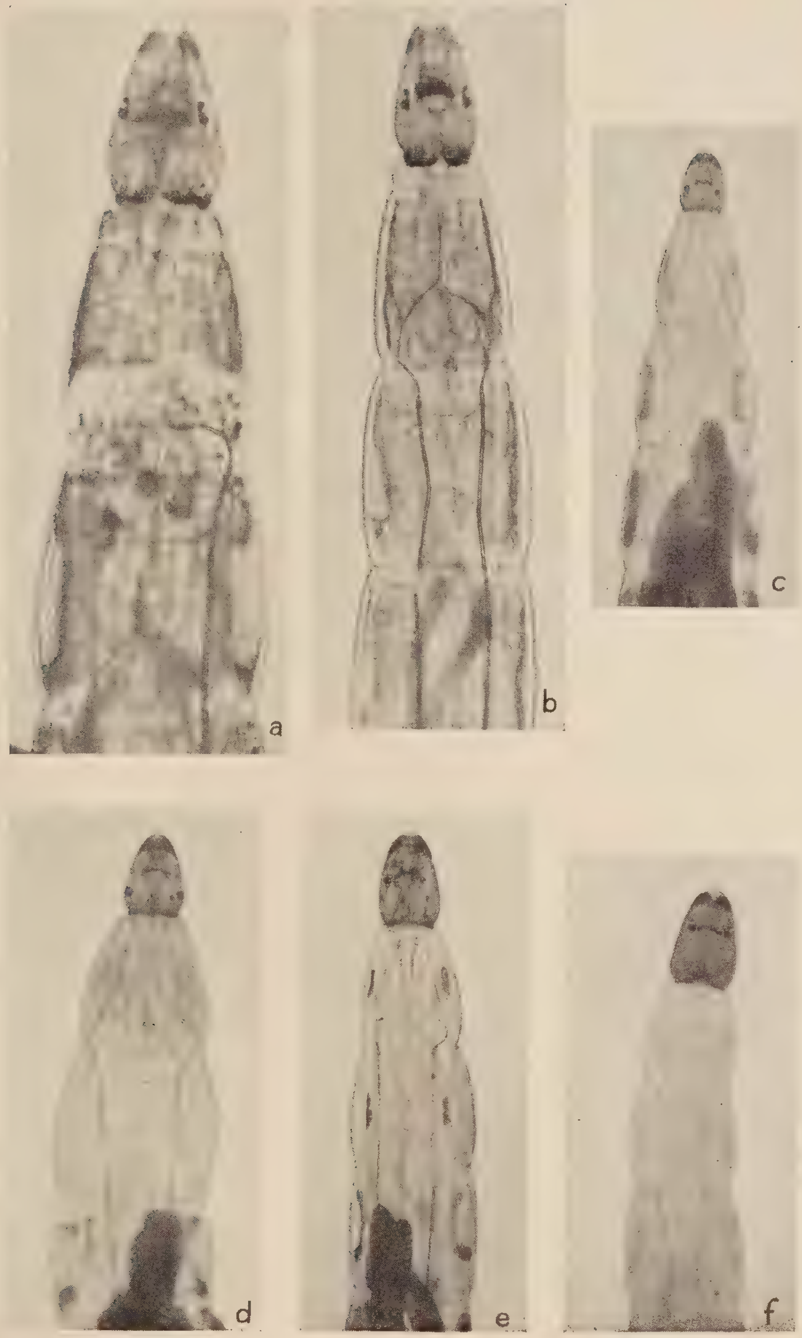
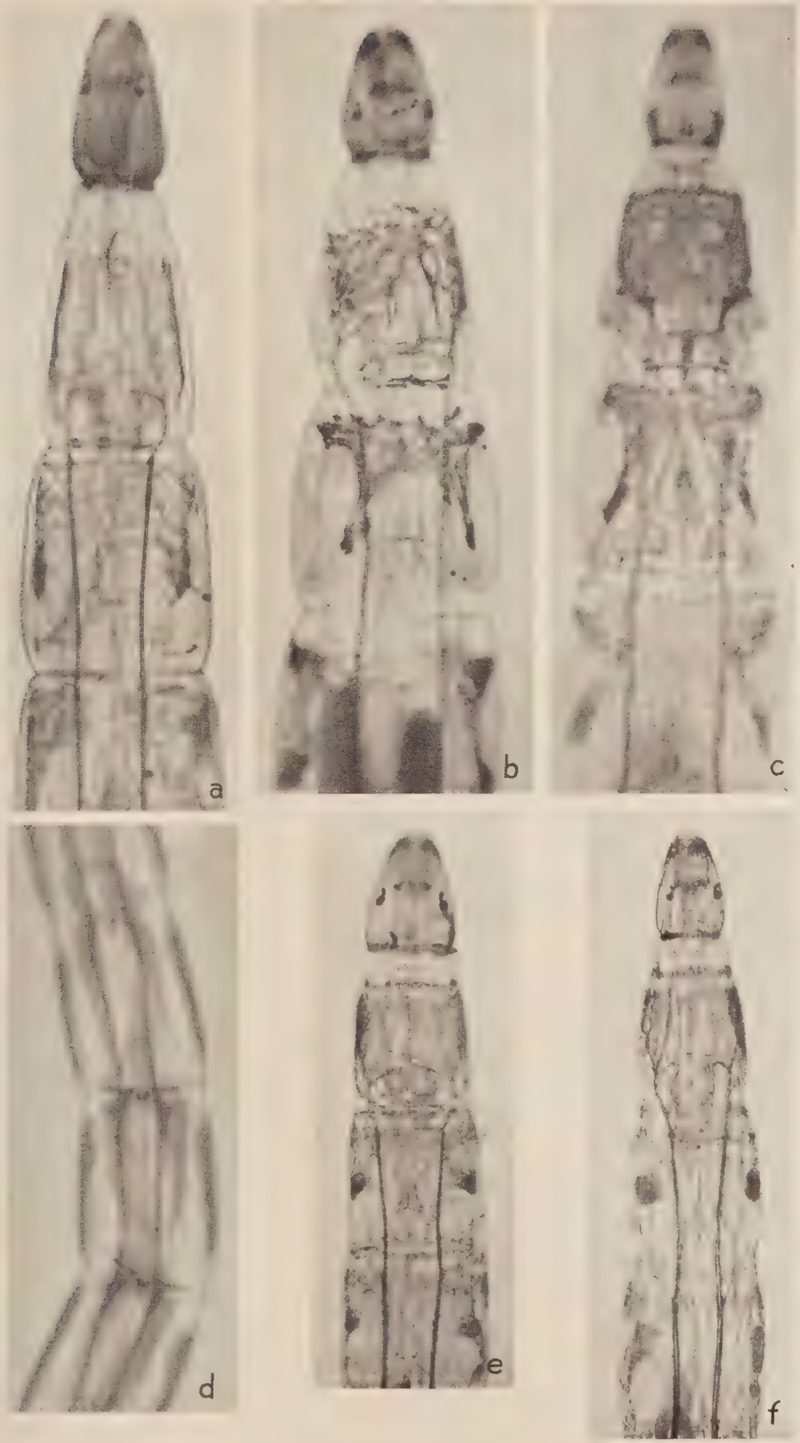
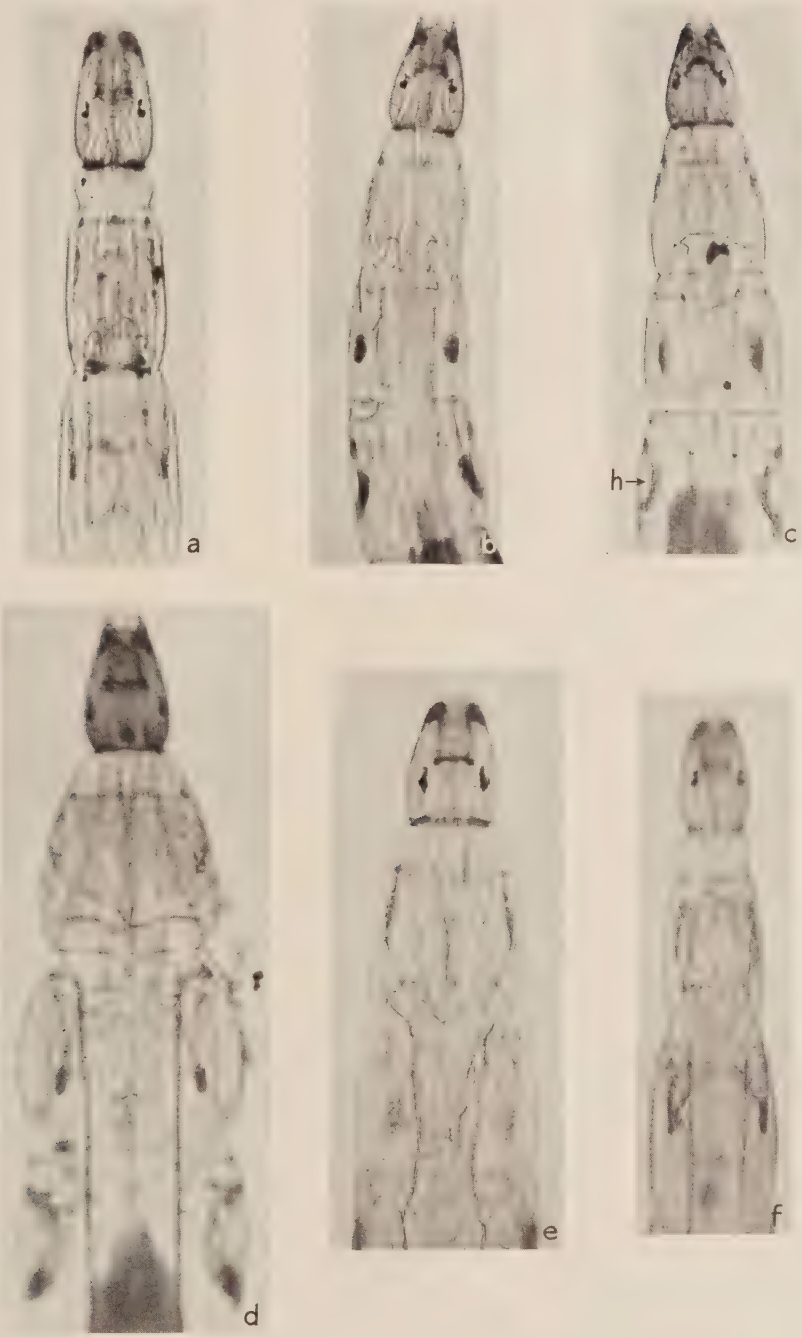


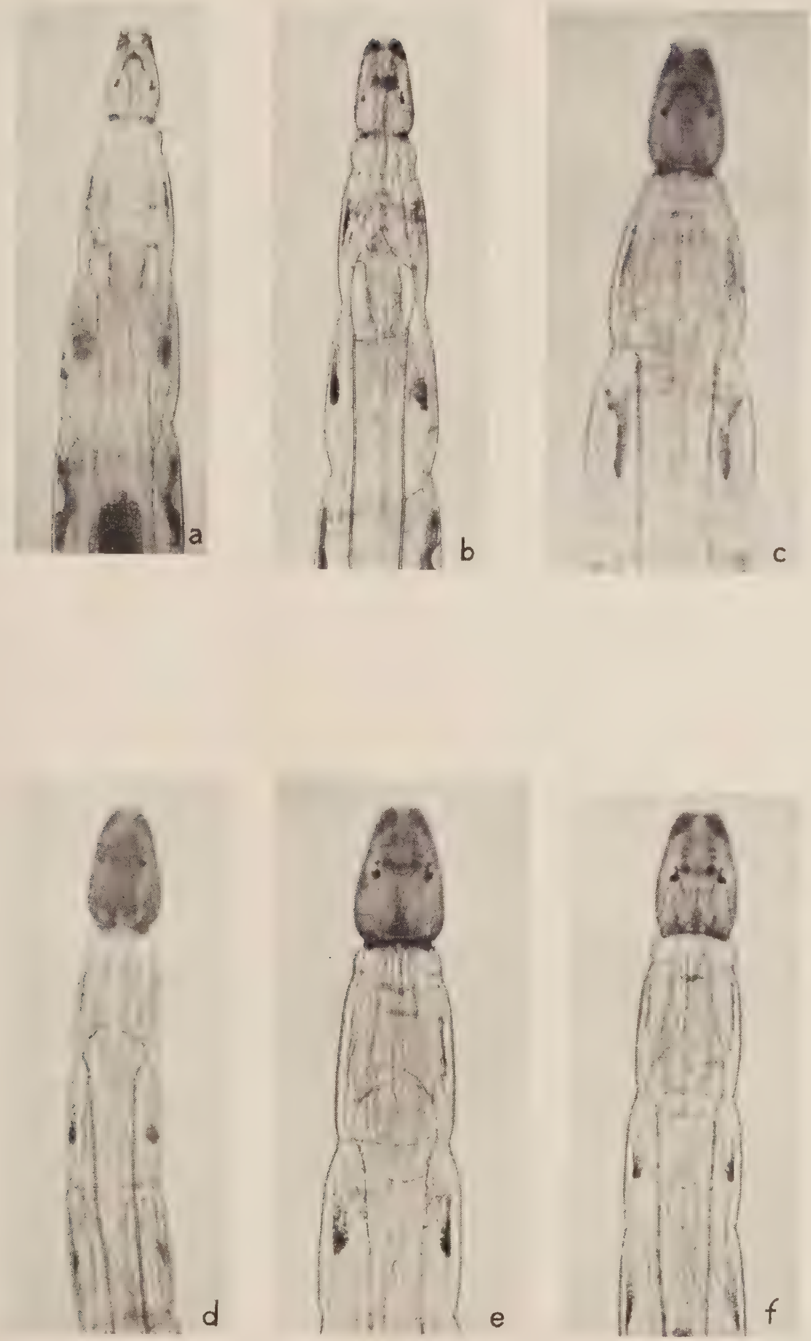
Head and thorax of (*a*), *C. nubeculosus;* (*b*), *C. stigma;* (*c*), *C. chiopterus;* (*d*), *C. scoticus;* (*e*), *C. obsoletus;* (*f*), *C. pseudochiopterus.* (All x 74).



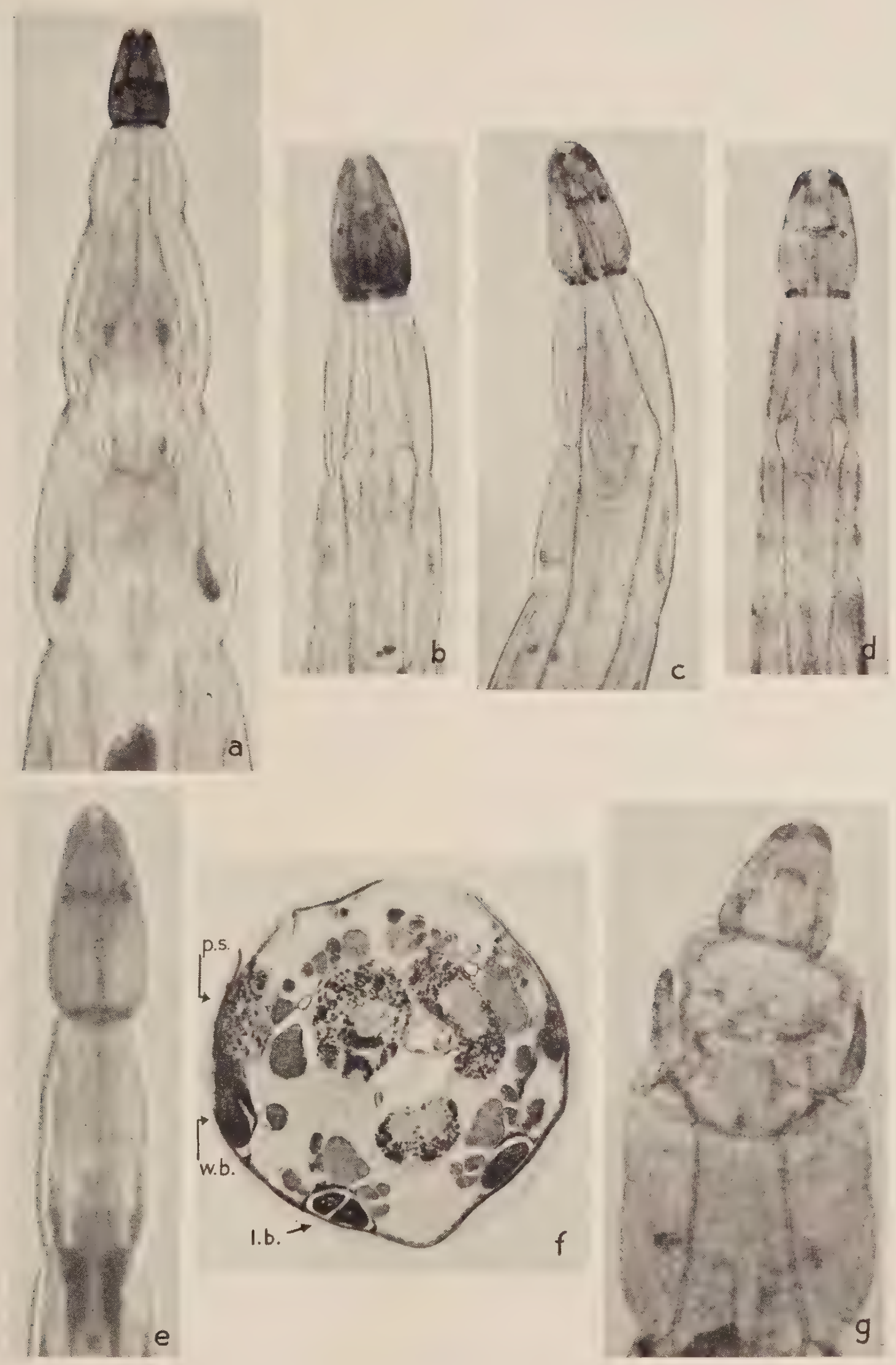
Head and thorax of (*a*), *C. lupicaris;* (*b*), *C. vexans;* (*c*), *C. circumscriptus;* (*d*), *C. salinarius,* part of the 4th instar abdomen showing markings; (*e*), *C. salinarius;* (*f*), *C. odibilis.* (All x 74).



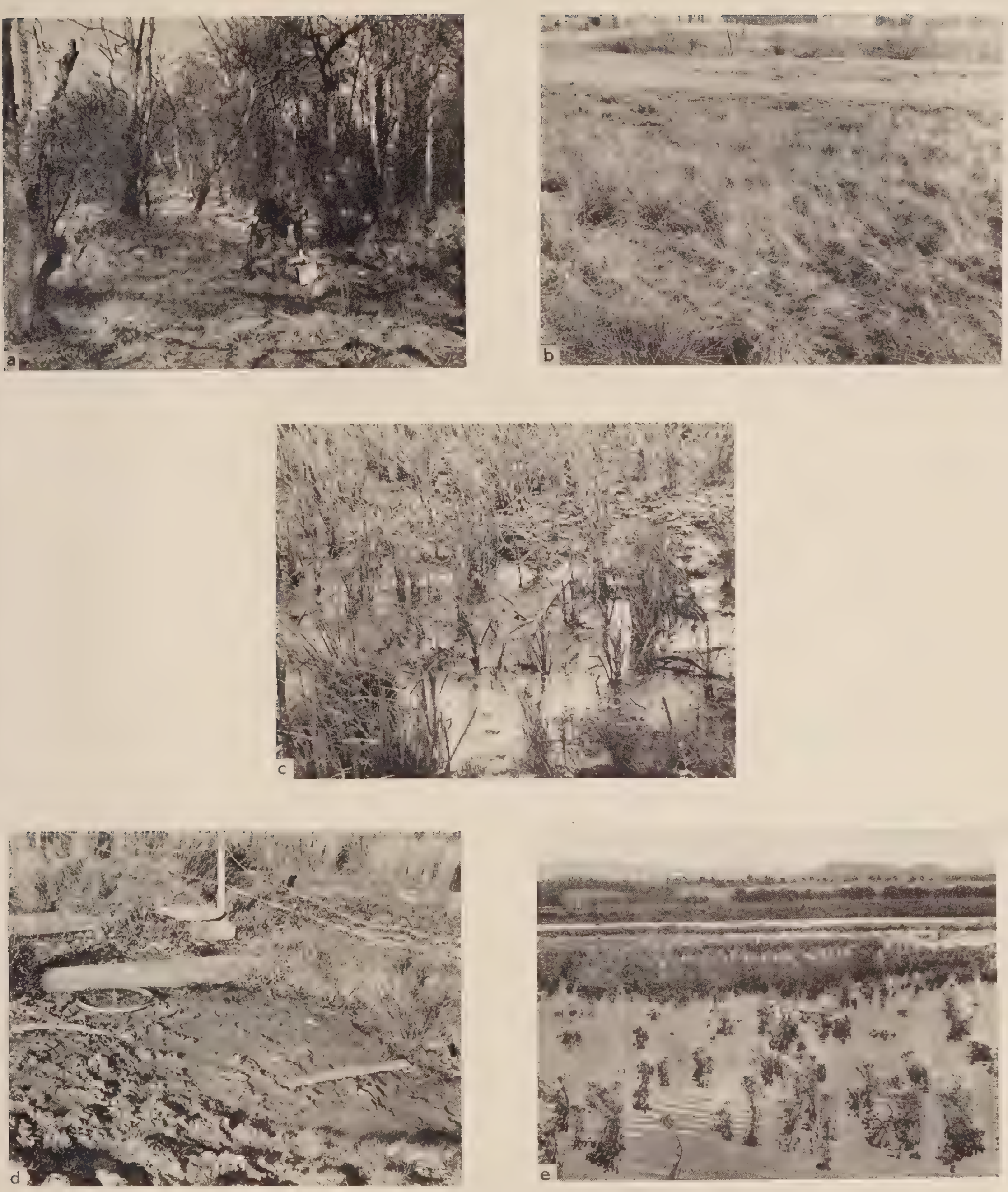
Head and thorax of (*a*), *C. albicans;* (*b*), *C. truncorum;* (*c*), *C. pallidicornis;* (*d*), *C. fascipennis;* (*e*), *C. pictipennis* (This specimen is rather flattened); (*f*), *C. maritimus.* (All x 74).



Head and thorax of (*a*), *C. cubitalis* (Note ectoparasites on head and " neck "); (*b*), *C. heliophilus;* (*c*), *C. halophilus;* (*d*), *C. impunctatus;* (*e*), *C. pulicaris;* (*f*), *C. punctatus.* (All x 74).



Head and thorax of (*a*), *Serromyia femorata;* (*b*), *Stilobezzia* sp.; (*c*), *Ceratopogon* (*Ceratopogon*) sp. head slightly distorted; (*d*), *Ceratopogon* (*Isohelea*) sp.; (*e*), *Bezzia* sp.; (*f*), *C. odibilis,* transverse section through the mesothorax of a 4th instar larva, showing the pigment spots (p.s.), the imaginal buds of the wings (w.b.) and legs (l.b.); (*g*), *C. albicans,* larva immediately prior to pupation. (All x 74).



(*a*) Bogland breeding place of *C. impunctatus* at Baldernock, Glasgow. The ground flora is composed of *Sphagnum* spp. and *Juncus articulatus* ' sensu lato '.

(*b*) Marshland breeding site at Drumchapel, Glasgow. *C. cubitalis* and *C. pallidicornis* are abundant among the rushes in the foreground, while on the open mud in the middle distance *C. odibilis, C. stigma* and *C. lupicaris* abound.

(*c*) Swamp breeding site at Drumchapel, Glasgow. *C. odibilis, C. pulicaris* and *C. punctatus* are found among *Carex riparia.*

(*d*) Muddy breeding site of *C. circumscriptus, C. stigma, C. nubeculosus* and *C. odibilis* at East Fleet, Dorset.

(*e*) Salt marsh breeding site of *C. salinarius* and *C. halophilus* at Beauly, Inverness-shire. The photograph was taken at high neap tide when only the heads of the sea-aster, *Aster tripolium,* broke the surface.

THE DEVELOPMENT OF EGGS OF *SCHISTOCERCA GREGARIA* (FORSKÅL) IN RELATION TO WATER.

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The development of Acridid eggs has been the subject of numerous recent investigations. Slifer (1949) studied, in particular, the changes in the permeability of grasshopper egg membranes to water during egg development ; the inhibition of water by the egg was stated to be one of the factors inducing the end of diapause. The present investigation was aimed at increasing knowledge of the rôle of water in the embryonic development of the Desert Locust, *Schistocerca gregaria* (Forskål).

Material and Methods.

The majority of the eggs used for the experiments were deposited in moist soil in an irrigated banana grove in the Jordan Valley on the 27th May, 1945, by a medium-sized swarm. Each batch was collected in the field a few minutes after laying. For later experiments, eggs laid in the laboratory were used. In all, 30 batches were used, the eggs being placed all together in a common container and drawn upon at random. Every day, some 70 eggs were used for determination of their weight and specific gravity.

The eggs were brushed up from the sand with a dry brush and weighed in groups of ten on a torsion balance. Only eggs of completely healthy appearance were selected. Those used for determination of specific gravity were washed in distilled water, and all shrunken or otherwise unhealthy-looking eggs were removed. The rest were dried on a filter paper, placed for a minute in 70 per cent. alcohol, dried

TABLE I.

Normal development of eggs of *S. gregaria* at 27°C.

Time since ovi-position	Description of embryo	Weight of egg in mg.		Specific gravity		Average length of 10 embryos
		No. of eggs	Average (M±3 m)	No. of eggs	Average (M±3 m)	
1 min....		30	10·5			
3 min....		30	11·2			
30 min....		30	11·3	25	1·124±0·002	
24 hours	Pyriform germ band ...	30	11·5	29	1·112±0·04	
2 days...	Cranial part distinct ...	30	12·3	29	1·111±0·02	0·6
3 days...	Small embryo distinct ...	30	12·8	30	1·09 ±0·003	0·9
4 days...	Early anatrepsis	30	13·8	22	1·084±0·009	1·5
5 days...	Late anatrepsis	30	19·1	30	1·07	3·2
6 days	Katatrepsis in various stages	30	23·93±0·15	30	1·061±0·001	3·6
7 days		40	21·62±0·54	30	1·063±0·006	3·8
8 days...	Katatrepsis completed ...	36	23·6 ±0·54	35	1·058±0·003	4·3
9 days...	Rapid growth of embryo ...	35	25·9 ±0·36	36	1·056±0·003	6·2
10 days...	Head of embryo reaches anterior end of egg ...	35	23·3 ±0·36	35	1·057±0·0024	8·8
11 days...		36	24·3 ±0·29	36	1·057±0·0024	8·9
12 days...		36	22·1 ±0·12	32	1·057±0·0009	
13 days...		37	23·45±0·25	32	1·057±0·006	
14 days...	Hatching begins	24	24·6 ±0·3	23	1·057±0·009	

again and placed in a minute wire basket in various solutions of salt of known specific gravity (Bodine & Robbie, 1943). The eggs which floated were counted and considered of the same specific gravity as the salt solution. The eggs used once were killed in Bouin's fluid, dissected, and their embryos examined and measured.

Normal Course of Development.

Table I represents the normal continuous development of eggs kept in wet sand at 27°C. Two additional series of weighings were made in order to bring the total number up to 100 ; the results of these were similar to those shown in Table I.

The embryonic development of eggs at 27°C. proceeds as follows. Twenty-four hours after oviposition, a pyriform germ band appears posteroventrally in the egg. Twenty-four hours later, the cranial part of the embryo can already be distinguished. On the fourth or fifth day, the embryo accomplishes anatrepsis, and katatrepsis occurs during the sixth and up to the eighth day. Thus, the embryonic differentiation of *Schistocerca gregaria* is similar to that of *Locusta migratoria* (L.) (Roonwal, 1936) and *Melanoplus differentialis* (Thos.) (Slifer, 1932).

Influence of Temperature.

Three series of experiments were arranged, each with about 90 eggs laid in the laboratory and incubated at temperatures of 15, 20, 27, 30, 33 and 37°C. In two series, the eggs were kept on wet filter paper and in the third in wet sand (Table II).

TABLE II.

Incubation of eggs of *S. gregaria* at different temperatures.

Temp. in degrees centigrade	15	20	27	30	33	37
Days (mean)	–	45–50	14–15	12	11	–
Percentage hatched ...	0	25	70–90	70–90	10	0

Hatching of the eggs kept in the wet sand was better than that on the filter paper. At 27–30°C., the percentage of eggs hatched was high, but at 33°C. and 20°C. only a small proportion hatched.

Hamilton (1950), investigating the effect of temperature on the incubation period of eggs of *S. gregaria*, came to the conclusion that there is a gradual reducton in the period of incubation with rise of temperature. His results were as follows :—

80°F. (26·7°C.)	... ...	16·0 days
90°F. (32·2°C.)	... ...	13·8 ,,
100°F. (37·8°C.)	... ...	12·5 ,,

The results obtained in the present investigation differ slightly from Hamilton's, as he hatched eggs successfully at 37·8°C. Bodenheimer (1929) hatched them at 40°C. On the other hand, in the present work, eggs of this species were hatched at 20°C., a temperature lower than those reported by both these other investigators. At this temperature, the egg remains lighter in weight, and does not become ready for katatrepsis until after the 12th day (Table III).

Influence of Water.

In discussing what happens to eggs which do not receive any water from their environment, Hamilton (1936) stressed the need to distinguish between 100 per cent. R.H. of the atmosphere and the direct contact of eggs with water-soaked material (sand, filter paper).

TABLE III.

Development of eggs of *S. gregaria* at 20°C.

Time after oviposition	Description of embryo	Weight of egg in mg.	No. of eggs
3 hours		9	20
1 day		9	20
2 days		9	20
9 days		11·2	10
11 days		12·0	10
12 days	End of anatrepsis	13·4	10
16 days	Katatrepsis begins	19·4	10
21 days		20·0	10
30 days		19·4	10
40 days		18·6	10
45 days	Hatching	18·0	5

In the work now described, experiments were carried out in glass tubes open at both ends, with a cotton-wool plug in the centre of each tube. These tubes were inserted into test tubes in which the relative humidity was controlled by the use of various chemical compounds. The compounds used and the corresponding humidities were as follows : H_2O, 100 per cent. ; KNO_3, 91–90 per cent. ; KCl, 85–83 per cent. ; NaCl, 74–71 per cent. ; $Ca(NO_3)_2$, 53–50 per cent. ; $CaCl_2$, 31–29 per cent. ; $ZnCl_2$ (saturated solution), 18 per cent. ; P_3O_5 (dry powder), 0 per cent. In spite of all the precautions taken, it is probable that some condensation of water vapour on the eggs occurred.

Two series of experiments were undertaken to determine the fate of eggs at various temperatures and air humidities when not in contact with water (Table IV). The eggs were one day old at the outset. They were examined daily and classified as dead when conspicuously shrunken ; such shrinkage did not reverse on moistening

TABLE IV.

Duration of survival, in days, of eggs of *S. gregaria* at various temperatures and relative air humidities, and not in contact with water. (Initially 20 eggs in each lot.)

Temperature in degrees centigrade	Relative humidity (per cent.)					
	40	60	70	80	90	100
20	4·5	4·7	5·4	5·5	5·0	5·4
25	5·1	4·8	5·2	5·2	5·0	5·1
27	4·0	5·0	5·8	6·0	19·1	95·0
30	4·6	5·4	5·6	5·1	13·3	24·7

All the eggs died within six days after oviposition except those at 100 per cent. R.H. and a few at 90 per cent. and 27–30°C. Some kept at 27°C. and 100 per cent. R.H. were dissected and several embryos were found in various stages of anatrepsis ; others failed to hatch when wetted 95 days after laying. This result should be compared with Table I, which shows that the embryos in eggs kept at the same temperature of 27°C. but in contact with water are in the stage of late anatrepsis and ready to revolve in five days, having already imbibed a quantity of water nearly equal to their initial weight.

In similar experiments, Bodenheimer (1929) studied two series of eggs which had undergone one-third and two-thirds of their development, respectively ; the eggs of the first series were able to develop at 80–100 per cent. relative humidity, and those of the second series even at 20 per cent. Hamilton (1936) repeated the experiment with eggs four and ten days old ; the eggs of the first series failed to hatch, whereas 80–100 per cent. of those of the second hatched. Neither author stated the embryological stage of the eggs.

TABLE V.

Effect of various temperatures and air humidities on eggs of *S. gregaria* incubated for five days, and not in contact with water.
(+) eggs hatched ; (−) failed to hatch.

Degrees centigrade	Relative humidity (per cent.)			
	40	60	90	100
20	+	+	+	−
27	−	+	+	+
30		+	+	+

The next experiment was carried out with eggs of known embryological stage in order to ascertain whether the amount of water already taken in would enable them to develop not only under conditions of water equilibrium, but even if they became liable to lose water (because of reduced humidity). Eggs five days old, in which the embryos were ready for katatrepsis, were divided into lots of 20 and were incubated under different conditions (Table V). The eggs at 100 per cent. R.H. and 20°C. were destroyed by mould. The results confirm the view that only eggs that have absorbed enough water to accomplish katatrepsis are able to develop without contact with water.

In order to find out at what stage a temporary interruption of development is possible, and how long it can continue, three series of experiments were carried out as follows.

(*A*) Eggs kept in contact with water were transferred to 100 per cent. R.H. at regular intervals. In this experiment, the water absorbed in three or four days of contact sufficed for hatching (Table VI). As it appeared curious that three-day-old

TABLE VI.

Eggs of *S. gregaria* kept after oviposition in wet sand and subsequently transferred to 100 per cent. R.H. and kept with no water in contact with them (200 eggs in each lot ; temperature, 27°C.).

Duration of contact with water (days)	Time from transfer to complete development (days)	Average total duration of development (days)
3	11	14
4	13	17
5	11	16
5	9	14
7	7	14
10	5	15
12	4	16
14	2	16
16	(control)	16

eggs had imbibed the quantity of water required, an additional experiment was undertaken, in which three batches of eggs were kept for three days after oviposition in moist sand and then transferred to 100 per cent. R.H. This experiment was repeated twice (Table VI). A sample of eggs was dissected before the beginning of each experiment and the embryological stage noted. Only a few eggs hatched, the majority having died during katatrepsis. Some embryos ready for hatching died inside the eggs, although the membranes split. The experimental eggs hatched some days later than the controls, but those transferred to the controls 17 and 24 days after the transfer to 100 per cent. R.H. hatched at the same time as those kept at 100 per cent. R.H. throughout.

TABLE VII.

Eggs of *S. gregaria* kept in wet sand for three days after oviposition and subsequently transferred to 100 per cent. R.H. (Three batches in each experiment ; temperature, 26·1°C.)

Developmental stage at beginning of experiment and number examined (in brackets)	Weight of eggs in mg. at time of transfer and number weighed (in brackets)	Kept in 100 per cent. R.H.		Controls kept on plaster of paris	
		Number of eggs hatched	Average time of incubation in days	Number of eggs hatched	Average time of incubation in days
Pyriform germ band (7)	13 (30)	1*	30	3	30†
Cranial part distinct (6) Small embryo (2) ...	10·6 (30)	5‡	31	6	21
Pyriform germ band (5)	11 (30)	11	31	5	18·2

*Two more embryos ready to hatch.
†Transferred to the controls 17 and 24 days after the beginning of the experiment.
‡Many more embryos started to hatch and then died.

Thus, some eggs which imbibed only a very small quantity of water were able to hatch, although the majority died during katatrepsis or failed to hatch after completing development.

(*B*) Eggs kept at 100 per cent. R.H. were transferred at intervals to contact with water, in order to find out how long the eggs retain their viability at 100 per

TABLE VIII.

The effect of keeping freshly laid eggs of *S. gregaria* at 100 per cent. R.H., but not in contact with water, and later transferring them to contact with water. (Three egg pods in each lot ; temperature, 27°C.)

Number of days at 100 per cent. R.H.	Number of days from transfer to complete development	Total duration of development in days
5	11	16
6	11	17
10	11	21
15	11	26
20	no development	
30	,, ,,	
60	,, ,,	

cent. R.H. and 27°C. when not in contact with water. Eggs kept in these conditions for six days and then dissected contained embryos in late anatrepsis, the stage which is normally reached after five days at 27°C. (Table I). The prevention of absorption of water had not arrested development.

(*C*) Next, eggs were kept, for various periods after oviposition, in an atmosphere of 100 per cent. R.H., but not in contact with water, and were then transferred to contact with it (Table VIII). Development after wetting required exactly the same period (11 days) when the period before transfer was six, ten or 15 days as when it was five days. Clearly, development can proceed without imbibition of water up to the stage of late anatrepsis, but for completion of it more water must be absorbed. If water is not provided within 15–20 days, the embryo dies.

Discussion.

The eggs of *S. gregaria* are able to develop at 20–33°C., if during 3–5 days following oviposition they absorb sufficient contact water to permit katatrepsis. Developing eggs normally absorb about their own initial weight of water. At 27°C., the water intake is slow during the first four days. A rapid gain in weight begins on the fifth day, when the embryo is in the stage of late anatrepsis, the rate of increase being greatest during the beginning of katatrepsis. The maximum weight of an egg that develops normally is about 27 mg., but some eggs weighing only 16 mg. may also hatch under conditions of contact moisture. These weights represent increases of 170 per cent. and 60 per cent., respectively, of the original weight. Experimentally, it is possible to obtain fully developed embryos, and even for some of them to hatch, from eggs weighing as little as 11 mg.

Salt (1949), who studied the water intake in eggs of *Melanoplus bivittatus* (Say), also found that the total amount of water absorbed was about 60 per cent. of the original weight of the egg, and that about 88 per cent. of the total absorption occurred during anatrepsis. If little water is lost subsequently, the eggs are still able to hatch.

Studying the conditions of development of *Dociostaurus maroccanus* (Thunberg), Bodenheimer & Shulov (1951) came to the conclusion that the exact timing of water intake is one of the principal factors of egg development. In *Dociostaurus*, loss of water in the initial stage of egg development appears to be obligatory, as is its intake when the egg is morphologically and physiologically ready for katatrepsis.

Salt (1949) has stated that if the eggs of *M. bivittatus* are denied contact moisture from the time of oviposition, they develop to the end of anatrepsis and remain viable for long periods, provided desiccation is not severe. When contact moisture is provided, such eggs hydrate very rapidly and continue development with a retardation of two or three days. Extra moisture from the environment is essential for the revolution of the embryo.

The experiments described in this paper demonstrated that, in the absence of contact water, the embryo of *S. gregaria* develops until late anatrepsis and remains alive in this stage for two weeks, but that it then requires contact water if further development is to take place. Although the quantity of water imbibed by contact is usually high, it is possible for eggs that imbibe only a small quantity in the first three days to complete their development and sometimes to hatch.

It is possible that under natural conditions, a long interruption of development may occur at 27°C. and lower temperatures. Such an interruption, together with the slow rate of development at 20°C., may account for prolongation of the period between oviposition and hatching up to 87 days (Ballard & others, 1932) and for the case reported by Husain & others (1940) when eggs of *S. gregaria* remained alive in dry soil for 81 days and resumed their development when the soil was moistened.

The developmental stage at which such an interruption takes place in the eggs of *S. gregaria* is identical with that in which embryos of other Acridids undergo diapause ; it is that of late anatrepsis, when the addition of water induces the commencement of katatrepsis, as reported for *M. bivittatus* (Salt, 1949) and *D. maroccanus* (Bodenheimer & Shulov, 1951).

Summary.

The course of embryonic development of *S. gregaria* under controlled conditions of temperature and humidity is described, with special attention to the water requirements of the developing egg. The development of the egg is interrupted if contact water is lacking and is resumed when the egg is moistened. This occurs at the stage of late anatrepsis, which is the stage at which the embryo of some other locusts and grasshoppers undergoes diapause.

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A NEW GALL MIDGE PREDATOR OF MEALYBUGS, *COCCOMYZA DONALDI* (DIPTERA : CECIDOMYIIDAE).

By A. Earl Pritchard.

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During a study of the natural enemies of mealybugs that transmit a virus causing swollen shoot disease of cacao, R. G. Donald submitted specimens representing a new species of the gall midge genus *Coccomyza*. This species is here described to provide a name for use in connection with the biological work.*

The genus *Coccomyza* has previously been known on the basis of a single species, *C. brittini* Del Guercio (1918), that is predacious on a gall-making mealybug in New Zealand. The new species, from the Gold Coast, Africa, is predacious on the mealybug, *Pseudococcus bukobensis* Laing.

Coccomyza donaldi, **sp. n.**

C. donaldi differs from *C. brittini* principally in that the tenth sternite of the male genitalia is truncate distally rather than deeply and widely emarginate, and the flagellum of the female is 12 segmented rather than 11 segmented (as illustrated by Del Guercio). Del Guercio described only ten flagellar segments in the female of *C. brittini*, but it is noteworthy that adults of this genus were recognised only from specimens contained in mature pupae.

Male.—Eye bridge wide, the mediolateral facets somewhat more distantly placed. Palpus four segmented, the segments successively increasing in length and the fourth segment slender and tapering. Antenna with 2+12 segments ;

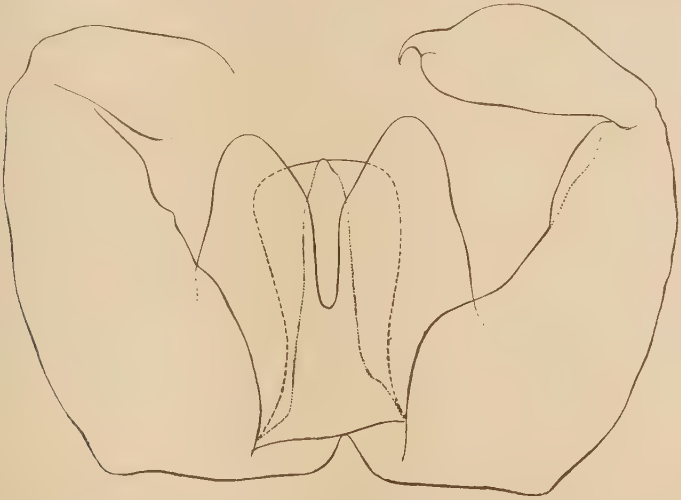

Fig. 1.—Hypopygium of *Coccomyza donaldi* ; holotype male.

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*According to Dr. H. F. Barnes of the Rothamsted Experimental Station, another as yet undetermined gall midge belonging to the Trifila sub-tribe of the tribe Cecidomyiariae occurs as a predator of *Pseudococcus citri* (Risso) and *P. njalensis* Laing on cacao in West Africa and must not be confused with *C. donaldi* which falls in the tribe Dasyneuriariae.—Ed.

pedicel subquadrate, smaller than scape ; flagellum without articulation between first and second segments ; each flagellar segment with a large proximal enlargement and a slender distal stem about one-third as long as enlargement ; terminal segment simple, obovate. Wings hyaline, covered with narrow, curved setae ; R_5 reaching tip of wing. Legs covered with lanceolate scales ; claws strongly bent and each with two small teeth proximally. Hypopygium with tenth tergite (dorsal plate) deeply cleft, the cleft narrowly divergent on proximal one-half and strongly divergent distally, slightly longer than basiforceps ; tenth sternite (ventral plate) spatulate, truncate distally and not quite as long as tenth tergite ; tegmen slender, gradually narrowing from base on proximal portion, angulate distally, as long as tenth sternite ; basiforceps broadly expanded and rounded on inner, proximal side, and broadly separated proximally ; distiforceps broadest post medially and with a strong, retrorse, terminal spur. Length of wing, 1·1 mm.

Female.—Similar to male except for antennae and genitalia. Antenna with 2+12 segments ; first and second flagellar segments united ; flagellar segments each slightly decreasing in length, and all segments with short but distinct distal stems ; terminal segment obovate. Ovipositor with ninth sternite somewhat longer than broad ; lamellae each consisting of a single, pear-shaped but slender segment. Length of wing, 1·2 mm.

Holotype : Male, Wiawso, Gold Coast, Africa, November, 1949 (*R. G. Donald*), predacious on *Pseudococcus bukobensis* Laing ; in the Pritchard collection.

Paratypes : One male, four females, Wiawso, Gold Coast, November, 1949 (*R. G. Donald*), predacious on *Pseudococcus bukobensis* Laing.

This species is named in honour of R. G. Donald of the West African Cacao Research Institute, because of his interest in the gall midge predators of mealybugs.

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THE LARGE-SCALE CONTROL OF THE COTTON JASSID IN THE GEZIRA AND WHITE NILE AREAS OF THE SUDAN.

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and

J. Taylor.

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(Plate XX.)

This communication discusses the analysis of many valuable yield records which have gradually accumulated in the Gezira and White Nile cotton areas of the Sudan since the beginning of large-scale chemical control of the Cotton Jassid, *Empoasca lybica* (de Berg.). A map of the area is given elsewhere (Cowland & Edwards, 1949).

Reliable data on which to calculate (*a*) the damage caused by pests and (*b*) the resultant value of control measures are seldom available, despite the importance of this aspect of agricultural economics for which Chester has recently reviewed the position in regard to plant diseases (Chester, 1950). The results described below would appear, therefore, to have a wider import than their practical value to the cotton industry in the Sudan, as they are the first carefully compiled yield increase data over a number of years for an agricultural spraying operation in tropical Africa. In addition, they show the rapid progress which an extensive organised agricultural industry like the Gezira Scheme can compress into a short space of time. Such schemes may have drawbacks, but there are undoubtedly great virtues. With a multitude of small independent farmers, the Gezira would never have surmounted the crisis arising 20 years ago from blackarm and leafcurl diseases ; and the lesser, although important, ravages of the Jassid would probably remain unabated.

The yield records and other data for the Gezira Scheme are probably unparalleled in tropical agriculture, and the management took the utmost pains to obtain the greatest possible information from the spraying operations against the Jassid. It was clear either at the time or in retrospect that much more information could have been obtained if it had been practicable to plan such major operations in the form of large-scale scientific experiments. It is, however, understandable that where the crop had to be irrigated fortnightly in strict rotation and the soil was only sufficiently dry for heavy spray machinery during the last few days before irrigation, a spraying programme within a limited period involved complex arrangements and hard work for everyone, not least the field executive of the Gezira Scheme. In addition, there were a variety of other factors, partly economic, which militated against a better distribution of spraying to cover all possible factors affecting responses by the crop. It is hoped that the present study, despite weaknesses, will be helpful in the Sudan and elsewhere.

THE GEZIRA SCHEME AND ABDEL MAGID.

Although the commercial cultivation of Egyptian cottons under irrigation in the Gezira Scheme began on a small scale of 250 feddans† at Tayiba (fig. 1, Block No. 12) in 1911, the crop had been grown experimentally some years earlier by Davie

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†One feddan = 1·038 acres = 0·42 hectare.

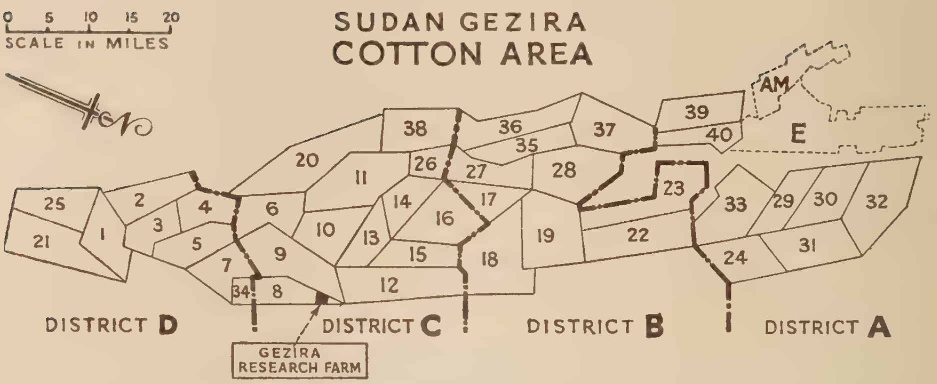

Fig. 1.

Block	Started	Block	Started	Block	Started	Approximate annual cotton areas	
						District	Feddans.
1 Ghubshan	1925	15 Abdel Galil	1925	29 Meilig	1930	D	37,000
2 Wad Naaman	1925	16 Wad Saadalla	1925	30 Kab el Gidad	1930	C	58,400
3 Hosh	1921	17 Abdel Rahman	1926	31 Turabi	1931	B	54,700
4 Remeitab	1921	18 Nidiana	1925	32 Laota	1931	A	56,600
5 Wad el Attaya	1925	19 Wad Sulfab	1925	33 Debeiba	1935	AM	10,000
6 Kumor	1925	20 Radma	1926	34 Seed Farm	—	E	25,000
7 Hamad Nil	1923	21 Hag Abdalla	1927	35 Amara Kasir	1929		
8 Barakat	1914	22 Dolga	1928	36 Feteis	1929	The gross areas are approximately four to five times the above.	
9 Darwish	1923	23 Istrahna	1928	37 Keteir	1929		
10 Abdel Hakam	1925	24 Umm Degarsi	1928	38 Nueila	1929		
11 Medina	1925	25 Fahl	1936	39 Fawar	1936		
12 Tayiba	1911	26 Wad el Bur	1929	40 Turis	1937		
13 Seleimi	1925	27 Wad Hussein	1929	AM Abdel Magid	1937		
14 Tebub	1926	28 Rukn	1929	E Extension	1951		

at Kamlin (Hanna, 1950, p. 367). By 1924, the area of cotton had increased to 22,000 feddans. With the opening of the Sennar Dam in 1925, it reached 50,000 feddans, and it is at present approximately 232,000 feddans grown on 44 Blocks (for definition see Hanna, 1950, p. 359) of variable size.‡ Until recently, the Scheme was a partnership between Government, tenants and two companies—the Sudan Plantations Syndicate on 34 Blocks, and the Kassala Cotton Company on 6 Blocks. A map of the Scheme is given in fig. 1 which also indicates the year in which Blocks were opened ; it also includes the extension opened in season 1951/52.

Lying on the edge of the Scheme is Abdel Magid, with an annual area of about 10,000 feddans of cotton. This was started in season 1937/38 as an Alternative Livelihood Scheme for some of those dispossessed of riverain land on the White Nile when the Gebel Aulia Dam was completed.

For purposes of this paper the Scheme is divided arbitrarily into four districts A to D, from north to south.

Rainfall is confined to the period May to October, with a large proportion in July and August ; it decreases from south to north, with isohyets tending to run from north-east to south-west.

Cotton is sown in the second half of August, just after the peak of the rains and coincident with widespread growth of weeds. The Jassid, which is considered to be confined during the hot, dry season to small pockets in relatively few gardens under perennial irrigation, moves to the weeds and cotton ; its population increases to a maximum about the end of November (Cowland, 1947), roughly 13 to 15 weeks after sowing, and tends to be appreciably heavier in the north where summer rainfall is least (Hanna, 1950). Main flowering of cotton is from November to January (Crowther, 1941), and so it is not surprising that extensive damage to leaves such as is caused by Jassids has been found to react adversely on that part of the crop which matures from the later flowers.

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‡Including the recent extension of 4 Blocks = 25,000 feddans.

Although the Jassid is now known definitely to cause considerable loss of yield throughout the Gezira in some seasons, the gradual realisation of its depredations and its only recent control are in marked contrast to the histories of leafcurl and blackarm. From about 1930, the last two threatened to cripple the Gezira ; rapid control measures were needed, and were found. Overall yields became satisfactory from 1934/35 onwards, and for a time undoubtedly obscured to some extent the lesser, more insidious effects of " hopper burn " leaf damage caused by the Jassid or Cotton Leaf Hopper. However, even if the extent of this damage had been recognised earlier than it was, control might easily have had to await modern developments in the chemical control of pests.

Much of the northerly and westerly districts of the Gezira Scheme in which the Jassid is most in evidence was not opened until 1928 to 1931. Nevertheless, the pest was known earlier, and it occurred in sufficient numbers to be considered as a possible vector in the spread of leafcurl disease, in which connection the first investigation of the life history of the insect was made by Michelmore in 1929 (Crowther, 1948). In cage experiments with large populations, he noted the typical leaf damage to cotton. On the young leaves of Egyptian cottons the Jassids, when numerous, cause wilting of leaf margins at midday ; on older leaves there is a yellow marginal band, sometimes narrow, sometimes spreading well into the centre of the leaf, resembling sun-scorch. These marginal areas ultimately dry, disintegrate and leave a tattered periphery. Michelmore considered that in the commercial area the cotton crop was not hurt even if the insect was present in numbers which would probably cause serious loss on American cotton elsewhere. In the light of events this may seem remarkable, but it was only in 1946 that a visiting entomologist of wide experience was impressed by the apparent lack of damage to Egyptian cotton in the Tokar Delta by a considerable population of the same pest. If there is any moral, it is to utilise the ever-expanding modern range of insecticidal chemicals to maintain plots free from the pest to be examined, to compare the yield with control plots and thus to test actual losses in yield, as an additional method in applied entomological studies.

Since the Jassid was proved not to be a vector in the spread of leafcurl, and owing to the very low cotton yields of 1929/30, 1930/31, 1932/33 and 1933/34, the major attention of research was devoted for a number of years to the control of blackarm and leafcurl diseases. T. Trought, however, in a written communication informs the authors that on his first visit to the Northern Gezira in 1931, he had been impressed by leaf damage which, from his experience of Jassids in India, he attributed to this insect. In annual research reports from 1933/34 onwards there are numerous references to the Jassid, particularly in the northern district but also further south at the Gezira Research Farm at Wad Medani (Sudan, 1935–1940). At the latter place A. R. Lambert in 1935/36 postulated that damage by the Jassid had a very detrimental effect on the crop, and G. B. Portsmouth in the same season suggested that damage by this pest was one of the major causes of reduced vegetative growth and earlier maturation of cotton in the northern districts. In 1936/37 Lambert referred to the lack of records for the Jassid as a serious gap in the knowledge of the factors affecting growth and yield, and he started an experiment to try to measure the effect of insects, including the Jassid, on yield. In 1937/38 and 1938/39, Jassids were recorded as numerous, with some suggested damage as far south as the Research Farm. Good average yields tended, however, to obscure the importance of the pest.

In 1939 Trought, who himself considered that the Jassid caused appreciable damage, decided that the loss should be determined by spraying. In the process, he and Cowland re-examined some old records, and found that a cage experiment by the latter in the northern district in 1935/36 could be interpreted to indicate a loss of 58 per cent. from jassid infestation (Cowland, 1947). Owing to the outbreak of war, staff was short, and work was confined to a small cage experiment in which Bedford reported a loss of 29 per cent. from jassid infestation (Bedford, unpublished report, 1940).

In 1941/42, the first spraying experiment was carried out by Ruttledge at the Research Farm, using three applications of bordeaux mixture applied at fortnightly intervals from the end of October. The increase in yield was 11 per cent. (Cowland, 1947). Although small, it was in the right direction, and it was the precursor of other successful spraying experiments both at the Research Farm and in the northern district ; and to Trought and Ruttledge particularly must be given the credit for initiation of work which has led to successful large-scale control and to great financial benefits to the Sudan. It is a pleasure to recognise that they had the strong support of the Companies who were concerned to assess the position.

Further experiments in 1942/43 and 1943/44 with bordeaux mixture gave promising increases in yield, particularly in the north (Cowland, 1947) ; and at the invitation of the Sudan Government, Dr. W. E. Ripper, Managing Director of Messrs. Pest Control Limited, visited the Gezira in December 1944 to advise on the possibilities of power spraying (Cowland & Edwards, 1949). Small experiments were also carried out by him, and soon indicated that DDT—then new—was likely to be greatly superior to bordeaux mixture or similar materials. Arrangements were made for an initial trial of power spraying in the 1945/46 season in the northern district ; but before discussing this and the work of later years, a few comments seem worth while.

It has been suggested (Cowland, 1947 ; Cowland & Edwards, 1949 ; and Crowther, 1948) that the Jassid has either increased gradually over a period of years or particularly since about 1939. There would now seem to be considerable evidence to the contrary. The observations mentioned above suggest that the pest was causing appreciable damage in and from at least 1931. Further information is provided by the very close correlation between seasonal yields and two rainfall factors in the period from 1933/34 to 1945/46. Arising from work by the late F. Crowther, E. M. Crowther and A. Gaitskell, it was found that variations in the average seasonal cotton yields of the Gezira Scheme in the 11-year period 1935/36 to 1945/46 could be related very closely to two rainfall factors. Rainfall in the pre-sowing period 1st July to 15th August was a beneficial factor, whereas total rainfall in the previous year was adverse. A period of 11 seasons is short statistically, and the close correlation may perhaps have been fortuitous. But even if fortuitous, the general level of yields appeared relatively stable. This indicates that Jassid had remained of constant importance over the period, even though incidence was seasonally variable and perhaps linked in some way with rainfall. Finally, infestations of cotton which may annually attain a high population have been considered to arise from a carry-over of the pest in the dead season in relatively few small gardens, quick movement in the rains to weeds and thence to cotton ; a quick build-up in any new area opened to irrigation is therefore possible and, in fact, happened in the northern district. Recently, Joyce (unpublished) has suggested that immigration from outside is partly responsible for the build-up on cotton ; there is no reason to suppose that these conditions have altered radically. In short, no biological factors are yet recognised to suggest a gradual increase in population over the years or a later sudden increase.

Power Spraying in Season 1945/46.

This has been described (Cowland & Edwards, 1949). In the northern Gezira, 1,650 feddans of cotton were sprayed either with copper oxychloride or with DDT emulsion, both in 100 gallons of water per feddan. Similar areas nearby had been selected beforehand as controls.

A very substantial increase of 1·59 k.p.f.* (40 per cent.) over a yield of 3·94 k.p.f. on control plots was obtained on Domains Sakel* variety at Kab el Gidad with mainly 0·1 per cent. but some 0·05 per cent. DDT emulsion (respectively 1 lb. and 0·5 lb. technical DDT per feddan) applied principally between 1st and 10th November. Somewhat earlier spraying in the same area between 20th and 28th October with 0·5 per cent. Blitox (a formulation containing 42 per cent. copper oxychloride) gave a much smaller increase of 0·43 k.p.f. (11 per cent.) over a yield of 3·90 k.p.f. on controls. The superior result with DDT was associated with a better and more sustained kill.

At Abdel Magid between 11th and 18th November, on X1730A variety, the increase from 0·1 per cent. DDT was 0·76 k.p.f. (24 per cent.) over a yield of 3·20 k.p.f. on control plots ; and at Turis on Domains Sakel variety spraying with 0·1 per cent. DDT between 20th and 25th November gave a still smaller, although profitable, increase of 0·42 k.p.f. (14 per cent.) over a control yield of 2·95 k.p.f. Observations in both these areas indicated that appreciable damage had already been caused prior to spraying.

The value of a cotton crop is decided partly by quality. With Egyptian cotton in the Gezira the grade falls fairly consistently from the first pickings to the last. Since the Jassid damages the leaves and causes premature cessation of growth, it is not surprising that the increased yield from spraying was found in the later pickings and lower grades, with no alteration in the top grades. Nevertheless, it was clear that control of Jassid with DDT had a future.

In addition, although small-scale experiments had been based on spraying carried out at, and after, the end of October, it appeared possible that the optimum spraying date might be earlier. Just how early it could start, and over what period it should ideally and could practically be concentrated, were problems for solution. An ideal period in chemical control often has practical disadvantages, for example, the number of machines required for a very short campaign may be excessive and overheads unduly high. Finally, would new problems arise, such as an increase in other pests through destruction of their natural enemies by DDT. The evolution of strains of insects resistant to DDT had not yet been envisaged.

The Yields of Sprayed Areas in the Gezira, 1946/47 to 1949/50.

From 1946/47 onwards a considerable area of cotton in the Gezira Scheme has been sprayed each season with DDT. The yield records of the Blocks in which spraying took place have been examined. These records give the area (normally 10 feddans) and the yield of the holding of every tenant, as well as the variety of cotton, the sowing date, whether nitrogenous manure was applied, the date and method of any spraying, and a note on any operations which differed from the standard practice. The statistical methods employed in the analyses are described in a note which has been deposited in the archives of the British Museum (Natural History), London.

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*K.p.f.=kantars per feddan ; 1 kantar=315 rotls (or 312 lb.) of seed-cotton, yielding approx. 100 lb. lint of Domains Sakel or 107 lbs. of X1730A.

Domains Sakel is the highest quality Egyptian cotton grown in the Sudan. X1730A is a leafcurl resistant selection of slightly lower quality, but higher ginning-outturn.

Basis of Analysis.

From the records of each season a summary was prepared for each Block* in which any spraying had been done. This divided up the treated area in each Block into sub-divisions according to (*a*) whether it was manured or not, (*b*) the method of spraying and (*c*) the date of spraying normally expressed in standard 10- or 11-day periods. The total area and yield for each sub-division were calculated. In the rare cases where both Sakel and X1730A varieties were grown in a Block, a separate summary was prepared for each. If a tenancy was not uniformly treated in respect of manuring and spraying, or if some non-standard practice such as fallow-hoeing had taken place, it was not included in the summary.

Inevitably, the arrangement of spraying " treatments " in the field did not correspond to any standard statistical design. However, it is roughly true that it was a matter of chance which treatment was applied to a particular piece of land ; and a Block containing on the average about 5,000 feddans of cotton may be regarded as one of the replicates of a randomised experiment. This has been done in our analyses.

Limitations of the Analyses.

If there are two areas of cotton, *A* and *B*, adjacent to each other, there is a continued movement of adult Jassids from *A* to *B* and from *B* to *A*, as well as movement within *A* and *B*. After spraying, movement of Jassids from any local unsprayed cotton will cause gradual reinfestation. The increase in yield of sprayed plots may not be as great as would have been obtained if the whole Block were sprayed. At the same time movement into unsprayed cotton from the sprayed plots is diminished. Furthermore, responses at the earlier spraying dates relatively to the later ones may be penalised.

In this study manuring always means the application of nitrogenous fertiliser, but this may be ammonium nitrate, ammonium sulphate or nitro chalk. In each season the rates of application were adjusted to give roughly equivalent amounts of nitrogen, but the effects on yield were not necessarily the same. This may be expected to increase the variability of yields on manured land.

The policy is to manure inferior holdings in order to help the tenants of such land. This means that, if the response to spraying should depend on the basic fertility of the land, any comparison of responses on unmanured and manured land is biased.

It is understood that the earlier and better crops are the most likely to be sprayed. This might make the increase in yields due to spraying appear greater than it really is.

The combined status of other pests—thrips, whitefly, Pink and Egyptian bollworms—is probably altered to some extent.

The method of regarding each Block as a replicate means that the estimates of variability used in testing significance are based on the discordance, between Blocks, in the observed increases due to spraying. They can only be used to test whether a hypothesis is true for a set of Blocks, and not for any individual Block. Also for this reason, all estimates quoted are means over a number of Blocks, which are identified.

The method of weighting observations, described in the following section, cannot be regarded as exact. However, it is probably the best practicable one.

All these limitations show that no great accuracy can be expected, that results must be very general, and that there are sources of bias the magnitude of which cannot be assessed. However, many of the results of the analyses are so clear-cut that their importance seems undoubted, though all numerical values given should be used with caution.

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*The word " block " is commonly used in statistical language to denote a replicate of an experiment laid out in a particular way. Where that meaning is intended in this paper it is written with a small " b" . Where it appears with a large " B " it means one of the sub-divisions of the Gezira Scheme (see Hanna, 1950, p. 359).

Power Spraying in Season 1946/47.

Over 10,000 feddans of cotton in the northern Gezira were sprayed by tractor-drawn sprayers (Pl. XX, fig. 1) with 0·1 per cent. DDT emulsion at 100 gallons per feddan (1 lb. DDT per feddan), mainly in parts of Kab el Gidad, Turabi, Keteir, and Abdel Magid. Spraying commenced in the second half of October and continued until 25th November. The summary of yields for unmanured land at Kab el Gidad and Turabi Blocks, both in District A, is given in Table I. Analyses of other areas were not made. The earlier the spraying the better were the responses which ranged from 19 to 100 per cent.

TABLE I.

Season 1946/47. Effect of date of spraying with DDT emulsion.

Spraying between	Kab el Gidad			Turabi		
	Area feddans	Yield k.p.f.	Yield % increase	Area feddans	Yield k.p.f.	Yield % increase
Oct. 21–31 ...	664	4.81	66	237	4·98	100
Nov. 1–10 ...	1,213	4·45	53	803	4·10	65
11–20 ...	840	4·06	40	500	4·00	61
21–30 ...	258	3·45	19	140	3·54	42
Unsprayed ...	4,834	2·90	—	6,230	2·49	—

k.p.f. = Kantars per feddan (see footnote on p. 483).

Concentrating attention on the figures for yield in kantars per feddan, we may regard them as the results of a randomised block experiment having two replicates and five treatments. We assume that each of them can be expressed as the sum of four components : (*a*) one representing the general level of all yields ; (*b*) one which is the same for all observations in a replicate, whatever the treatment ; (*c*) one which is the same for all observations of a particular treatment, irrespective of replicate ; (*d*) a random component, normally distributed. However, the areas differ so much that we cannot assume all the random components to be distributed with the same standard deviation, as is done in the ordinary analysis of variance procedure. It has seemed most reasonable to assume, for each analysis which we have done, that each observation is distributed with standard deviation $\frac{\sigma}{\sqrt{A}}$, where σ is the same for each observation and A is the area in feddans on which the yield is based. This is equivalent to giving each observation a " weight " equal to its value of A. It can only be regarded as an approximation to the truth, but it seems reasonable, intuitively.

Making this assumption, the components (*a*), (*b*) and (*c*) were estimated by the method of least squares. The components (*c*) are shown in the second column of Table II. These are the best estimates which can be made from the data, on our present assumptions, of the increase in yield due to spraying in each of the periods.

It is apparent that the yield fell off as the date of spraying became later, and it may be surmised that the yield was a linear function of the date of spraying, and that the irregularities in the estimated components (the differences between successive values are 0·50, 0·29 and 0·56, so are not all equal) can be ascribed to the random variation always to be expected. This was assumed and the method of least squares

TABLE II.

Season 1946/47. Components of yield due to treatments, Sakel cotton on unmanured land.

Treatment	Component (*c*) (k.p.f.)	Component, assuming linear relation (k.p.f.)
Sprayed, Oct. 21–31	2·09	2·04
Sprayed, Nov. 1–10	1·59	1·64
Sprayed, Nov. 11–20	1·30	1·23
Sprayed, Nov. 21–30	0·74	0·82
Unsprayed	0·00	0·00

was then used to estimate the components afresh, the results being given in the third column of Table II. Strictly speaking, the analyses should have allowed for the fact that the period 21st to 31st October includes 11 days, but each of the other periods 10 days only. The error introduced by assuming all periods to be equal in length will be small compared with the errors from other sources, and the computations were greatly simplified by ignoring it. A test of significance showed that the components in the second column did not fit the original data significantly* better than those in the third column. We therefore accept the hypothesis that yield was a linear function of the date of spraying.

A more convenient method of presenting the results, for comparative purposes, is used in Table III (which also includes figures for two subsequent seasons). This gives the estimated decrease in yield for each day by which spraying was postponed, and it gives the estimated increase in yield of sprayed over unsprayed cotton for various dates of spraying. It also gives a weighted mean yield for unsprayed cotton, as an indication of the general level of yields.

TABLE III.

Estimated effect on yield of Sakel cotton due to spraying with DDT emulsion, 1946/47 to 1948/49 (all yields in k.p.f.).

Season		1946/47	1947/48		1948/49	
Whether manured		No	No	Yes	No	Yes
Blocks included in analysis ...		30, 31	24, 29, 30, 31, 32, 33, 37, 39, 40	24, 29, 30, 31, 32, 33, 39, 40	18, 22, 23, 24, 28, 29, 30, 31, 32, 33, 36, 40	22, 23, 24, 28, 29, 30, 31, 32, 33, 36, 40
Decrease in yield per day ...		0·041	0·036	0·030	0·017	0·016
Increase in yield obtained by spraying on ...	Oct. 1	—	—	—	0·90	1·04
	Oct. 15	—	1·96	2·27	0·66	0·82
	Nov. 1	1·81	1·38	1·78	0·37	0·56
	Nov. 15	1·25	0·89	1·36	0·14	0·34
Mean yield of unsprayed cotton		2·69	2·26	2·57	3·51	3·75

Power Spraying in Season 1947/48.

The excellent yield increases in 1945/46 and 1946/47 justified expansion of spraying, and in 1947–48 over 39,000 feddans in the northern Gezira were treated, mainly with 0·1 per cent. DDT emulsion at 100 gallons per feddan, but partly with DDT wettable powder at the same concentration and volume. Spraying started rather earlier, and tractor-drawn sprayers were used as in previous years. Results were again excellent ; the average yield of sprayed cotton was 3·69 k.p.f. compared with 2·46 k.p.f. for unsprayed cotton in the same Blocks, an increase of 1·23 k.p.f. or 50 per cent.

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*All tests referred to in this paper were carried out using the $P=0{\cdot}05$ level of significance.

In the detailed consideration of results, account had to be taken of pre-sowing nitrogenous manuring which was starting after a wartime shortage of fertiliser. The rate of application in this season was about 60 r.p.f.* expressed as nitrogen (in 1948/49 and 1949/50 it was about 45 r.p.f.).

DDT emulsion on unmanured land.

The main spraying was with DDT emulsion on unmanured land and very largely on Sakel cotton. Statistical analysis was confined to the yields for Sakel, and was done in the same way as for 1946/47. The hypothesis that yield was a linear function of the date of spraying was found to fit the data adequately. The numerical estimates obtained are given in Table III. That the yield could be almost doubled by one spraying emphasised the damage which Jassid can inflict. Furthermore, in the early small scale experiments of 1941 onwards, treatments did not start until the end of October ; the results in 1947/48 serve as a forcible reminder of the necessity in experimental work to examine what at the time may be considered extremes.

Data for X1730A cotton were wholly insufficient for any conclusions on the responses to spraying relative to those of Sakel. The yields for X1730A at Abdel Magid were, however, examined ; earlier spraying seemed superior :—

Sprayed Oct. 13–Nov. 2 ...	2,340 feddans	3·72 k.p.f. (144%)
Sprayed Nov. 3–Nov. 25 ...	2,495 feddans	3·49 k.p.f. (135%)
Unsprayed	4,510 feddans	2·58 k.p.f. (100%)

DDT emulsion on manured land.

In this case the control was unsprayed but manured land. The areas involved were much smaller and were confined to 8 Sakel Blocks. The hypothesis that yield was a linear function of the date of spraying was again found to fit the data adequately and the numerical estimates obtained are given in Table III. However, the estimated increases in yield are greater for manured than for unmanured land. A statistical test showed that this effect was not significant at the P=0·05 level, though it was not far from it. If it were really true that the increase was 0·31 to 0·47 k.p.f. greater, as is estimated, it would be a fact of considerable economic importance. It is worth recording that an experiment at Abdel Magid with X1730A cotton gave the same indication, although not significant statistically :—

	Feddans	k.p.f.	
No nitrogen, unsprayed	295	2·89	diff. 0·85
No nitrogen, sprayed	300	3·74	
Nitrogen, unsprayed...	150	2·94	diff. 1·12
Nitrogen, sprayed	150	4·06	

DDT wettable powder.

About 1,900 feddans in 5 Blocks were sprayed with a 33 per cent. DDT wettable powder formulation at the rate of 100 gallons per feddan of a suspension containing 0·1 per cent. technical DDT, which was obviously very effective. Comparisons of yield, valid as regards date of spraying and other factors, indicated that there was little or no difference from emulsion :—

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*r.p.f.=rotls per feddan, roughly pounds per acre.

	Feddans	k.p.f.
DDT emulsion	1,060	4·16
DDT wettable powder ...	1,102	4·11

Cotton grade.

In 1945/46, an analysis (Cowland & Edwards, 1949) indicated that the increase of yield from spraying came in the later pickings and lower grades,* while the top grades were unaffected. During an investigation in early 1949 on the problem of grade itself, a very full analysis was made for Debeiba Block in 1947/48, when little land was manured but about half was sprayed against Jassid. Some of the results are given in Table IV.

TABLE IV.

Effect of spraying on cotton grade.
Debeiba Block 1947/48 (unmanured land).
Yields in kantars per 10 feddans, Grades 1–6.

	Sowing date, August	Fed-dans	Grade						Total
			1	2	3	4	5	6	
Unsprayed... ...	15–28	3,135	·40	4·95	5·77	3·97	5·30	6·44	26·83
Sprayed	15–28	2,972	·99	7·64	7·93	4·21	10·15	9·87	40·79
Unsprayed... ...	16–20	1,350	·42	5·27	5·81	3·44	5·76	6·99	27·69
	21–25	1,584	·43	4·21	5·60	4·67	5·10	6·37	26·38
Sprayed in Oct. and Nov.	16–20	1,222	1·13	10·15	8·91	4·09	9·61	9·08	42·97
	21–25	1,288	1·07	5·62	7·71	4·71	11·24	11·11	41·46
Sprayed in Oct. ...	16–20	907	1·18	10·88	8·86	4·06	9·01	7·80	41·79
	21–25	794	1·08	5·56	8·12	4·39	12·15	11·51	42·81
Sprayed in Nov. ...	16–20	315	·97	8·05	9·05	4·17	11·34	12·77	46·35
	21–25	494	1·05	5·72	7·04	5·21	9·77	10·48	39·27

Spraying gave an increase in yield distributed over every grade.

Much of the crop was sown in the 10 days between 16th and 25th August which for more detailed study were divided into two 5-day periods. The first sowing period was associated with very slightly better yields with and without spraying ; without spraying the grades of the two periods were similar, but with spraying the grade of the first period was slightly better.

Subdividing the two sowing periods for spraying in October and November, respectively, results became more variable, but there was a tendency towards rather poorer grade with the second sowing period. There was no definite indication that date of spraying was important as regards grade.

All differences were secondary to the large effect of spraying, shown principally in increases of yield in Grades 2, 3, 5 and 6.

Effect of locality.

All the Blocks used in the statistical analyses to give the results for 1947/48 in Table III belong to District A, except for unmanured Sakel land of Block 37 in

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*The seed-cotton before ginning is classified in six major grades, 1 to 6, in descending order of quality.

District B where spraying with emulsion was early and increases in yield were considerable. On Block 35 (X1730A, District B) all spraying was late, but there was a 20 per cent. increase in yield.

Other spraying in 1947/48 was confined to Blocks 36, 28, 22 and 18—all Sakel except in 36 ; the spraying was late. As Table V shows, results were variable.

As a whole it appeared that Jassid caused appreciable damage in District B in 1947/48.

TABLE V.

Season 1947/48. Trial late spraying with DDT emulsion in District B.

Block	Date Nov.	Sprayed		Control		Note
		Area feddans	Yield k.p.f.	Area feddans	Yield k.p.f.	
36	19–26	1,191	3·56 (96)	5,868	3·71 (100)	Whole block
28	23–27	333	3·66 (137)	250	2·67 (100)	Special area
22	24–25	180	4·03 (133)	87	3·03 (100)	,, ,,
18	26	180	2·96 (103)	140	2·86 (100)	,, ,,

Power Spraying in Season 1948/49.

The successful results in previous seasons led to further expansion of the spraying work in 1948/49 when about 78,000 feddans were sprayed in the Gezira Scheme and 9,000 feddans at Abdel Magid. Both DDT emulsion and wettable powder and, in addition, some DDT paste were employed at the rate of 100 gallons of 0·1 per cent. technical DDT per feddan ; and a small area was treated by helicopter at low volume, 3 gallons of 3·3 per cent. technical DDT as emulsion per feddan. Work started earlier. More cotton was treated in District B, and trials were made in Districts C and D. Table VI gives the approximate distribution, which was not uniform ; more emulsion was applied in October than in November, and in October it was confined to Districts A and B ; except on a small area wettable powder and paste were both applied in November only.

TABLE VI.

Season 1948/49. Areas sprayed with DDT in 1,000 feddans.

District	October			November		
	Em.	W.P.	Paste	Em.	W.P.	Paste
A	30	—	—	15	3	5
B	7	—	—	10	3	1
C	—	—	—	2	—	—
D	—	—	—	—	1	—

Jassid counts by the Research Division of the Ministry of Agriculture indicated a much lower infestation than in previous seasons, and this was reflected in smaller increases of yield from spraying. At the same time the general level of yield on unsprayed land was much higher than in the previous seasons.

DDT emulsion on unmanured cotton : application by tractor-drawn sprayers.

Statistical analysis for the Sakel Blocks gave results very similar to those of 1947/48, except that the estimated increases were lower in magnitude (Table III). The data again conformed adequately with the hypothesis that yield was a linear function of the date of spraying. It will be noted that as spraying started in the 1st–10th October period an estimate is given for 1st October.

Although responses were relatively small, they had to be viewed against a high cotton price ; on this basis, even at the later dates, spraying as a whole was profitable in both Districts A and B.

DDT emulsion on manured cotton : application by tractor-drawn sprayers.

A statistical analysis for manured land in the Sakel Blocks gave results very similar to those for unmanured land. As in 1947/48, estimated increases in yield were greater for manured land, but this season the effect was very far from being significant. Nevertheless, it was estimated to be between 0·14 and 0·20 k.p.f., which if real would be important (Table III).

DDT emulsion : district and varietal effects.

Of the 12 Sakel Blocks taken for statistical analysis, seven are in District A, and five in District B. Rough calculations suggest that the increases due to spraying were rather greater in District B than in District A, perhaps by about 0·2 k.p.f.

At Abdel Magid in District A there appeared to be a substantial increase of 0·87 k.p.f. (27 per cent.) from spraying of 9,000 feddans of X1730A cotton in October and November.

Blocks 39 (District A), 35 and 37 (District B) and 38 (District C) grew X1730A cotton. A statistical analysis for unmanured land in these Blocks showed that sprayed areas gave rather greater yields than unsprayed areas, but not significantly so. Moreover, there was no sign of any relationship between the yield and the date of spraying. The weighted mean yield of unsprayed areas in these Blocks was 4·58 k.p.f., and the estimate of the (non-significant) increase in yield due to spraying was 0·22 k.p.f. The records of spraying on manured land in these Blocks were not sufficient to justify statistical analysis.

DDT wettable powder : application by tractor-drawn sprayers.

About 7,000 feddans were sprayed, mainly in November, with 50 per cent. DDT wettable powder, from two different sources. It may be remembered that in 1947/48 a 33 per cent. wettable powder was used.

An experiment was carried out in seven Blocks, in each of which an unmanured area of 90 feddans was sprayed with emulsion in the first half of November ; similar areas were sprayed with wettable powder on approximately the same dates, or left unsprayed. In six of the seven comparisons emulsion was superior. The average difference between formulations was small and not statistically significant, although it was considerable relative to the small general increase from spraying (Table VII).

TABLE VII.

Season 1948/49. Comparison of methods of spraying on unmanured land. Yields in k.p.f.

	Experiment		Routine	
Emulsion	4·52	0·23	3·76	0·16
Wettable powder	4·29		3·60	
Unsprayed	4·04		—	

Blocks used in " routine " analysis :—
Sakel : 23, 24+, 28, 29, 30, 31+, 32+, 33+, 40. *X1730A* : 37+, 39+.

The blocks marked +, and also Block 35 (X1730A), were included in the experiment.

A comparison of the two methods was also possible from the records of routine spraying. For each 10-day period, each Block in which some unmanured land had been sprayed by each method was regarded as a replicate. This gave 13 replicates in all, from 11 Blocks ; two Blocks each gave information for two periods. The data obtained were analysed in a similar way to the analyses described earlier, and an estimate was obtained of the difference in yields between cotton sprayed by the two methods—assuming this difference to be the same for any spraying date, and for either variety of cotton. As will be seen from Table VII, the difference was in the same direction to that shown by the experiment ; it was, however, not significant.

The source of supply for wettable powder was different from that in the previous season when there was little or no difference in yield between treatments with emulsion and wettable powder respectively (p. 486) ; such powders can vary considerably in efficiency, and it is considered possible that the 1947/48 supply was slightly superior. When each pound of cotton lint is valuable, consistent small differences in results even if not significant must be considered.

DDT paste.

The distribution of the spraying with paste was such as to give too few comparisons with emulsion ; paste may have been rather inferior. Its use was found to present practical difficulties.

Helicopter spraying.

About 2,000 feddans were sprayed by a Sikorsky S51 helicopter equipped with spraying gear, using the same DDT emulsion as used in tractor-drawn spraying, but diluted to 3 gallons per feddan. Available comparisons with ground application in the same periods were few, and tended to favour the helicopter spraying, but they were totally insufficient for a reliable assessment.

Cotton grade.

There was extensive bad opening of cotton in 1948/49. Examination of the data for grades in the large-scale experiment noted under wettable powder indicated, as expected, that spraying did not augment this phenomenon (Table VIII).

TABLE VIII.

Season 1948–49. Effect of spraying on grade of cotton.

Treatment	Feddans	Average yield k.p.f. in various grades						Total
		1	2	3	4	5	6	
Control	628	·02	·16	·35	·49	1·94	1·08	4·04
Emulsion ...	618	·03	·19	·36	·34	2·06	1·54	4·52
W. powder ...	625	·02	·22	·19	·51	1·96	1·39	4·29

The relatively small increases in yield from spraying were obtained in the later picked and lowest grade cotton.

Power Spraying in Season 1949/50.

The area sprayed in the Gezira was increased to about 137,000 feddans and extended to 35 Blocks plus Abdel Magid. Work started still earlier, in the last week of September. About 68 per cent. of the sprayed area was treated with the usual emulsion ; most of the remainder was sprayed with wettable powder, but substantial trials were included with emulsion at three-quarters and one-half the standard strength in 100 gallons per feddan. All except about 5,000 feddans were treated by ground machine. Pre-sowing nitrogenous manuring in the Scheme increased very considerably.

The various spray treatments were not distributed uniformly either in time or place, as can be seen from Table IX, which summarises the records used for analyses of application by ground machine. DDT emulsion was used more particularly in Districts A and B, and wettable powder employed further south at a rather later date in Districts B, C and D.

Jassid infestation was considerable throughout the area, and responses to spraying were good in all Districts.

At Abdel Magid all the cotton was sprayed.

TABLE IX.

Season 1949/50. Cotton sprayed in the Gezira Scheme by tractor-drawn machines. Areas (feddans) used for analyses.

Spraying period	Unmanured land				Manured land			
	W.P.	E1	$E\frac{3}{4}$	$E\frac{1}{2}$	W.P.	E1	$E\frac{3}{4}$	$E\frac{1}{2}$
Sept. 21–30 ...	—	2,393	—	—	—	1,640	—	—
Oct. 1–10 ...	—	9,370	—	—	—	5,942	—	—
11–20 ...	200	15,819	—	—	—	8,247	—	—
21–31 ...	448	15,018	—	—	180	10,095	—	—
Nov. 1–10 ...	3,389	3,903	2,831	2,742	1,566	2,822	2,151	2,185
11–20 ...	6,129	2,559	—	—	4,492	1,618	—	—
21–30 ...	400	246	—	—	383	430	—	—
Total	10,566	49,308	2,831	2,742	6,621	30,794	2,151	2,185

District	A	B	C	D	Total
W.P.	1,502	2,575	11,840	1,270	17,187
E.1	35,848	28,502	12,248	3,504	80,102

W.P. = Wettable powder.
E.1 = Emulsion at full (1) and lower rates ($\frac{3}{4}$ and $\frac{1}{2}$).

Emulsion at standard strength on unmanured and manured cotton: application by tractor-drawn sprayers.

A rough estimate was first made of the average increases of cotton yield from spraying in the four Districts, irrespective of variety; Table X gives the data obtained for unmanured land. Good responses to spraying were obtained in all Districts. A striking feature was the apparent constancy of response at all dates.

TABLE X.

Season 1949/50. Approximate increases in yield of cotton in k.p.f. from spraying with standard strength emulsion on unmanured land.

District	Sept. 21–30	Oct. 1–10	11/20	21/31	Nov. 1–10	11/20	21/30	Unsprayed k.p.f.
A ...	1·30	1·92	1·86	2·60	1·86	1·18	—	3·10
B ...	2·82	1·63	1·40	1·46	1·53	1·53	—	3·40
C ...	—	1·69	·78	1·31	1·41	1·73	·53	3·53
D ...	—	—	—	1·51	1·66	—	—	3·78
All ...	1·60	1·76	1·53	1·86	1·58	1·56	·53	—

	Sakel Blocks	*X1730A Blocks*
A	24, 29, 30, 31, 32, 33, 40	39
B	18, 19, 22, 23, 27, 28, 35, 37	27, 36
C	12, 14, 16	6, 9, 10, 11, 13, 14, 20, 38
D	— — —	2, 4, 5

The same Blocks were used for a statistical analysis ; all except Nos. 2, 27 and 40 provided information for manured as well as unmanured land.

A separate analysis was made for each variety on unmanured and manured land. Each of these four analyses showed that spraying gave a significant increase in yield, but that there were no significant differences between dates of spraying. In other words, the data could be represented adequately by the hypothesis that in any Block the true yield was the same for every date of spraying, but greater for sprayed cotton than for unsprayed. This will be discussed later.

A rough investigation suggested that the increase in yield due to spraying was different in different Districts. A separate analysis to estimate the increase was therefore made for every variety—manuring—district combination. The results confirmed that the increases differed significantly between Districts. Moreover, they showed that the increase for any variety—manuring—district combination could be adequately represented as the sum of two components, one characteristic of the variety—manuring combination and the other characteristic of the District.

(*a*) *Components due to variety and manuring, k.p.f.*

	Sakel	*X1730A*
Unmanured ...	1·49	1·73
Manured ...	1·66	2·23

Components due to district

District A	+0·20 k.p.f.
District B	+0·11 ,,
District C	−0·28 ,,
District D	−0·43 ,,

Yields of unsprayed areas ranged from 1·8 to 4·5 k.p.f. according to variety, manuring and district.

Thus, the best estimate of the increase in yield due to spraying Sakel on unmanured land in District A is $1{\cdot}49+0{\cdot}20=1{\cdot}69$ k.p.f. That due to spraying X1730A on manured land in District C is $2{\cdot}23-0{\cdot}28=1{\cdot}95$ k.p.f.

For Sakel, it is estimated that spraying manured land gave increases 0·17 k.p.f. greater than spraying unmanured land ; the difference is not significant. For X1730A, the difference is 0·50 k.p.f. and it is significant. This is the only time in analyses for three seasons that such an effect has been significant, but the sign of the effect has always been the same.

The decrease in the response to spraying as one moves south from District A to District D is, as has already been stated, statistically significant. Although notable, it is not unexpected since the Jassid is considered normally to decrease in numbers from north to south. The greater increase from spraying X1730A than Sakel is not unexpected ; the former is in general basically a higher yielding variety, and the tendency towards greater increases from manured cotton than unmanured is a rather similar effect. As Districts C and D mainly grow X1730A the smaller District component in 1949/50 was offset by a higher varietal component.

DDT emulsion at varying strengths.

In the period 1st–10th November some large trials were made with emulsion of 0·075 per cent. and 0·05 per cent. DDT at the rate of 100 gallons per feddan. A separate analysis was made for unmanured and for manured land, for each variety, to test whether the yields given by cotton sprayed at these rates differed significantly from one another and from those of cotton sprayed at the standard strength. The following Blocks supplied data for the analyses :—

Sakel :—	12, 16, 22, 23, 28, 31, 32, 37, 40.
X1730A :—	2, 4, 5, 6, 9, 11, 15, 27, 39.

Block 2 provided information for unmanured land only ; Blocks 5 and 23 for manured land only.

None of the analyses showed the differences between the three strengths to be significant. A combined analysis for both varieties and for both unmanured and manured land also showed no significance. It may be mentioned, however, that the combined analysis estimated the yield to be 0·09 k.p.f. lower for 0·075 per cent. DDT, and 0·24 k.p.f. lower for 0·05 per cent. DDT, than for the standard strength. Once again there is an effect which is not significant but which could be important if the true value were the same as the estimate.

DDT wettable powder : application by tractor-drawn sprayers.

Almost all the spraying with 0·1 per cent. DDT wettable powder at 100 gallons per feddan took place in November. It employed principally 33 per cent. material similar to that used in 1947/48, together with a little 50 per cent. material from 1948/49. The records of routine spraying were used to compare the yields of areas sprayed with emulsion and wettable powder in the same Blocks in the same 10-day periods, as in 1948/49. A separate analysis was made for unmanured and for manured land for each variety. Three of the analyses showed no significance, nor any suspicion of it ; but the analysis for X1730A on manured land showed that the yield was significantly greater, at the P=0·01 level as well as P=0·05, for emulsion. The estimated differences are given in Table XI. In each case it is estimated that emulsion gave a higher yield.

TABLE XI.

Season 1949/50. Comparison of methods of spraying. Estimated difference in yield in k.p.f. between cotton sprayed with 0·1 per cent. DDT emulsion and that sprayed with 0·1 per cent. DDT wettable powder.

	Sakel	X1730A
Unmanured	0·20	0·07
Manured	0·01	0·79

Blocks included :—Sakel : 14, 16, 18, 19*, 22*, 23†, 29*, 31, 32, 35*, 37, 40*.
X1730A : 2*, 4, 6*, 9*, 10, 11, 13, 20, 27, 36*, 38, 39*.
Information for : * unmanured land only, † manured only.

There is no obvious explanation of the anomalous result for X1730A on manured land. Roughly half the area included in that analysis was in one Block (38, Nueila) which gave large differences between the methods, but the same Block did not give particularly large differences for unmanured land.

Helicopter spraying.

Almost the whole of Turis Block and a small part of Fawar Block, about 5,000 feddans in all, were sprayed by a Sikorsky S51 helicopter equipped with spraying gear and using DDT emulsion at low volume. Increases of yield were good but available comparisons were far too few for assessment against ground application.

Power Spraying in Season 1950/51.

Through the kindness of the Sudan Gezira Board we have been supplied with some preliminary figures compiled by Mr. A. C. Dennison for season 1950/51, when, as a result of exceptionally good seasonal rainfall factors, widespread manuring and spraying, a record yield of 6·8 k.p.f. was obtained. Jassid incidence was relatively light.

A total of 162,869 feddans in all Districts (excluding Abdel Magid) was sprayed with DDT emulsion and wettable powder during October and November, employing both tractor-drawn sprayers and Hiller helicopter (Pl. XX, fig. 2). The average increase in yield on sprayed land was approximately 0·65 k.p.f. Table XII gives averages in more detail, covering most of the area but with no allowance for variety, date of spraying, and other factors.

TABLE XII.

Season 1950/51. Some average yields in k.p.f. from spraying with DDT.

District	Manured land			Unmanured land		
	Sprayed	Unsprayed	Difference	Sprayed	Unsprayed	Difference
A	6·51	5·21	+1·30	5·45	4·88	+0·57
B	7·07	6·10	+0·97	6·49	5·91	+0·58
C	7·24	6·99	+0·25	6·80	6·45	+0·35
D	7·37	7·47	−0·10	6·56	6·70	−0·14
All	7·29	6·53	+0·76	6·34	6·05	+0·29

Although the figures are not strictly comparable between themselves, the yield increases are consistent with a relatively light jassid attack, decreasing from north to south and showing the usual indication of greater response to spraying on manured than on unmanured land. At present prices of cotton the yield increases in three Districts and in the Gezira as a whole were very lucrative. Without a detailed analysis it is impossible to say whether the negative responses in District D are significant ; but even if they are not, the result is worth bearing in mind.

An experimental comparison between 0·1 per cent. DDT as emulsion and wettable powder applied at 100 gallons per feddan was made in 27 Blocks. Wettable powder was superior in 14 cases, emulsion in 13 ; emulsion was superior in average yield but this is clearly not significant although following the usual trend :—

Emulsion ...	2,328 feddans	...	7·20 k.p.f.
Wettable powder	2,259 ,,	...	7·11 ,,
Unsprayed ...	2,357 ,,	...	6·70 ,,

Discussion.

(A). In general the Jassid population increases considerably during October and November. If the degree of yield-damage to cotton was purely dependent on the population of the pest, more damage would be expected from the feeding in November than in October. This was presumably the reason for confining the earlier small scale experimental sprayings to November and the end of October. However, results reported in this communication have shown that in seasons 1946–47, 1947/48 and 1948/49 yield was a linear function of the date of spraying, *i.e.*, damage caused in October was as serious as that caused in November, in spite of the much larger Jassid population in the latter month. This strongly suggests that the yield damage per Jassid was more in October than in November. The certainty of some reinfestation after early spraying is immaterial to the argument ; without it, the superiority of October spraying would presumably have been still greater.

Until at least the end of November the cotton plant in the Gezira is actively increasing in size (Crowther, 1941) ; not only is green leaf dry matter increasing, but the percentage of nitrogen in the leaf is decreasing. For such reasons the loss of a unit weight of leaf in October is presumably much more important than a similar loss in November. In short, during October and November, with an increasing number of Jassids, it is possible to visualise a decreasing yield-damage effect per Jassid. In the three seasons noted above the cumulative effects resulted in yield becoming a linear function of the date of spraying.

In 1949–50 there was no significant difference between the yield increases at various dates of spraying, which suggests that effective damage by Jassid did not commence until November. Counts made by Mr. C. J. Edwards, of Pest Control Ltd., between about 20th September and 10th October in 1948 and 1949 showed that in 1949 populations were very much less (one-half to one-tenth) than in 1948, although the infestation later in the season was considerable in 1949 and much less serious in 1948.

On the average of the four seasons it appeared definitely more lucrative to spray Sakel cotton in October than in November although, of course, the quantitative responses in the various seasons were different. There was insufficient evidence on which (*a*) to decide whether spraying could be started in September with good results since spraying only began as early as this in 1949/50, and (*b*) to assess whether X1730A cotton would have given the same qualitative results.

(B). Although the dates of major economic importance are those at which optimum responses in yield can be obtained from spraying it is of interest to know when no response is likely. If the figures in Table III are plotted on a graph the dates for no response are approximately :—

1946/47	Unmanured	Dec. 16		
1947/48	,,	Dec. 10	Manured	Jan. 1
1948/49	,,	Nov. 23	,,	Dec. 7

In practice the aim in all seasons was to finish spraying on or before 25th November.

(C). There were consistent but statistically non-significant indications that the increases in yield from spraying of Sakel cotton were greater quantitatively in the case of manured than unmanured land. The indications were about 0·39 k.p.f. in 1947/48, 0·17 k.p.f. in 1948/49 and 0·17 k.p.f. in 1949–50. For X1730A cotton in 1949/50 the difference was 0·50 k.p.f. and this was significant. It is not essential, although it may be correct, to invoke the aid of an increased Jassid population to explain such results. Nitrogenous manuring increases the nitrogen level in the leaves, and the effect on yield by a single Jassid will presumably be increased if it damages the same weight of leaf on manured as on unmanured cotton.

(D). The normal quantity of DDT as emulsion was 1 lb. per feddan. Only in early November 1949/50 was it compared with lower quantities, *viz.*, $\frac{3}{4}$ lb. and $\frac{1}{2}$ lb., all at the rate of 100 gallons per feddan. Although these lower quantities diminished the yield response, the effects were not significant.

(E). Similar comparisons were possible between 1 lb. of DDT per feddan as emulsion and wettable powder, respectively, mainly in November ; in only one case was there a significant difference, but in every case the difference was in favour of emulsion. The emulsion was standard throughout, but the wettable powders varied. The increases in yield obtained by the use of emulsion as compared with the wettable powder were as shown below :—

1947/48	·05 k.p.f.	(33% W.P.)
1948/49	·16 to ·23 k.p.f.	(50% W.P.)
1949/50	·01 to ·79 k.p.f.	(Chiefly 33% W.P.)

It is important to note that use of wettable powder was confined to November in which month rain is infrequent. Even so the standard DDT emulsion was always better. Nevertheless, it was satisfactory that differences were only small since wettable powders, unless carefully prepared, often compare badly with emulsions, and the emulsion used in the Sudan was especially formulated for the conditions.

(F). In 1948/49 and 1949/50 some spraying was carried out by Sikorsky S51 helicopter using standard DDT emulsion in less volume of water. The available comparisons with tractor-drawn sprayer were too few to enable any analysis ; there was every indication, confirmed by field counts of kills, that the helicopter spraying was good and on a par with that of the ground machines. Aerial spraying has two advantages ; firstly, it can be carried out when the land is wet and unfit for ground machines, and secondly, the irrigation ridges of the land do not have to be broken down to enable passage of machines. It is therefore unfortunate that no more than general indications of its efficiency relative to ground machines were possible.

(G). In no comparison made in 1945/46, 1947/48 and 1948/49 was there any evidence that spraying had any adverse effect on grade of the cotton crop. The increase in yield showed mainly in the bottom grades ; top grades remained relatively constant, but any effect on them seemed to be beneficial. It is important to note that in 1948/49 when there was much premature opening of cotton bolls, spraying had no adverse effect.

(H). For purposes of this analysis the Gezira was divided into four Districts, A to D, from north to south. It is approximately true to say that the two northern Districts A/B grew Domains Sakel variety and that the two southern Districts C/D grew X1730A variety. In addition it had been considered for many years that the Jassid tended to be more numerous in the north ; counts and small scale spraying experiments confirmed this view. Power spraying therefore commenced in the north. In 1947/48 it extended into District B in which results indicated that Jassid caused appreciable damage. In 1948–49 rough calculations suggested that the increases due to spraying were rather greater in District B than in District A. In 1949–50 spraying extended all over the Gezira. Analysis showed that damage decreased progressively from north to south ; but in District C where the Gezira Research Farm is situated the increase in yield of unmanured X1730A cotton was still about 1·45 k.p.f. Lambert was truly correct when in the mid-thirties he was disturbed at the lack of records for Jassids at the Farm. In 1950/51 a rough examination of the records suggests that damage again decreased progressively from north to south, although yield increases were on a smaller scale than in season 1949–50 and were absent in District D.

Considerably more evidence is still required on the seasonal extent of damage in the various Districts.

(I). There is also very little evidence on the relative responses of Domains Sakel and X1730A varieties to spraying. In 1949/50 the response of X1730A exceeded that of Sakel by 16 per cent. on unmanured land and 34 per cent. on manured land. More information is needed.

(J). The average yield of cotton for the Gezira Scheme without spraying from 1935/36 until 1945/46 was about 4 kantars per feddan or acre, roughly 1,200 lb. of unginned cotton or 400 lb. of lint plus 800 lb. of seed. An increase of only 1 per cent. in yield involves 4 lb. lint and 8 lb. seed per feddan, of considerable nett value when prices are high, quite apart from the importance in increased world agricultural production. It is often forgotten that the cotton plant produces a valuable oil-seed.

Even in 1948–49, a season of low jassid infestation, the increase in yield of Sakel cotton in District A reached 1 kantar with spraying in early October (Table III) ; in 1946/47 and 1947/48 it would probably have been over 2 kantars.

In 1949/50 some 137,000 feddans in the Gezira were sprayed at a cost of less than £200,000 ; the estimated increase in yield from the operation was 220,000 kantars, worth between £4,000,000 and £5,000,000. In 1950/51, a season with relatively light jassid attack, the estimated increase from 162,869 feddans in the Gezira (excluding Abdel Magid) was 105,000 kantars, and the price of cotton had risen sharply.

It is pertinent to remember that a loss of efficiency of only 1 per cent. in the spraying, due to factors such as less suitable chemical formulations or poorer application, can involve a loss up to 2 or 2½ lb. of lint, and 4 or 5 lb. of seed, per feddan.

It is also a striking reflection that 1 lb., even ½ lb., of DDT can lead to increased yields of over 200 lb. of lint and 400 lb. of seed.

(K). Only in a limited area was spraying carried out in every season. It is perhaps of interest to record in Table XIII the results for 4 seasons in Turabi and Kab el Gidad Blocks.

TABLE XIII.

Seasons 1946/47 to 1949/50. General yield increases for two blocks, expressed as percentages.

Date sprayed	Kab el Gidad				Turabi			
	46/47	47/48	48/49	49/50	46/47	47/48	48/49	49/50
Sept. 21–30 ...	—	—	—	—	—	—	—	39
Oct. 1–10 ...	—	—	37	77	—	—	56	43
11–20 ...	—	118	7	76	—	—	41	47
21–31 ...	66	78	7	65	100	—	27	71
Nov. 1–10 ...	53	44	19	—	65	61	16	47
11–20 ...	40	—	(−9)	—	61	46	5	14
21–30 ...	19	—	77	—	42	6	—	—
Unsprayed % ...	100	100	100	100	100	100	100	100
Unsprayed k.p.f. ...	2·90	1·96	3·69	2·95	2·49	1·79	2·51	2·38

(L). In the present 1951/52 season extensive areas have again been sprayed. When the yields are available it is hoped that a full examination will be made of the voluminous records for it and the previous season.

White Nile Schemes.

To the west of the Gezira Scheme there is a very appreciable area of irrigated cultivation of Egyptian cotton along the banks of the White Nile between Kosti and Gebel Aulia. The water is pumped from the river. Some of the cultivation is privately owned ; the rest consists of the Government scheme at Dueim and of four schemes started as an alternative livelihood for cultivators dispossessed of riverain flood cultivation by the Gebel Aulia Dam. This account refers to the latter, and yields from season 1939/40 are given in Table XIV.

Fatisa is the northernmost scheme, approximately in the latitude of the northern blocks of District B in the Gezira Scheme ; Umm Gerr is the most southern, in a latitude rather south of District D in the Gezira. In between, from north to south, lie Wad Nimr, Hashaba and Dueim. Rainfalls are lower than in the corresponding latitudes of the Gezira ; as already stated the isohyets have a north-east to south-west tendency. These schemes are typical of the White Nile banks in possessing extremes of soil, good and bad ; nevertheless, the general level of yields particularly in Hashaba and Fatisa became very disappointing and gave rise to considerable anxiety. Overcropping was suggested as the cause of the low yield. However, when the excellent results of power spraying in the Gezira in 1945/46 were known, it was realised that the prevalence of Jassid in Fatisa and Hashaba was probably largely responsible for the poor yields and it was decided to spray all cotton in these two schemes in season 1947/48, using 0·1 per cent. DDT emulsion at 100 gallons per feddan applied by tractor-drawn sprayer. In addition it had already been decided to manure with nitrogen to mitigate any overcropping. The results were most gratifying.

TABLE XIV.

White Nile Schemes.

Yields in kantars per feddan.

Variety—Domains Sakel except where marked with an asterisk (X1730A). The first season with spraying has a line drawn above it.

Season	Fatisa	Wad Nimr	Hashaba	Dueim	Umm Gerr
39/40	3·87	—	—	3·18	—
40/41	2·65	—	2·59*	3·71*	—
41/42	3·04	—	2·37	2·86	—
42/43	3·26	—	3·51	3·58	4·07
43/44	1·94	3·97	2·07	2·25	2·58
44/45	3·35	4·45	3·43	3·90	4·32
45/46	1·95	3·32	2·00	2·28	2·69
46/47	1·92	2·83	1·64	2·72	3·78
47/48	$\overline{3{\cdot}62}$	2·91	$\overline{4{\cdot}01}$	2·83	3·25
48/49	4·69*	$\overline{5{\cdot}81}$*	4·46*	$\overline{3{\cdot}75}$*	$\overline{4{\cdot}37}$*
49/50	4·48*	6·37*	4·32*	3·98*	4·67*
50/51	6·21*	9·30*	5·80*	5·59*	6·82*
First cotton in ...	39/40	43/44	40/41	28/29	42/43

In opening up a new area it is not unusual to obtain in the first season a particularly good cotton yield relative to the seasonal trend. Although the crop in the second season is also on new land, there is not the same enhanced effect. The reason presumably lies in the relative absence of certain pests and diseases in the first season. In 1947/48 the yield of Fatisa was not far below that of its first season ; and Hashaba gave a record yield ; both rose above the other schemes.

In both schemes, small areas remained unsprayed and this enabled a rough estimate of the effect of spraying which was greater at Hashaba (Table XV). Particularly at Fatisa, both sowing and spraying started earlier than in the Gezira, and it would seem that the optimum spraying period could have straddled the beginning of October. At Hashaba the effect of spraying date was marked as in the Gezira Scheme.

In season 1948/49 spraying was extended to all schemes including Umm Gerr which is less liable to serious jassid infestation. All land was manured and practically

TABLE XV.

Season 1947/48. Spraying with DDT emulsion.

Hashaba			Fatisa		
Spraying dates	Area feddans	Yield k.p.f.	Spraying dates	Area feddans	Yield k.p.f.
Oct. 3– 8 ...	284	4·77 (185)	Sept. 25–30	580	3·67 (132)
Oct. 9–14 ...	280	4·55 (176)	Oct. 14–18	504	3·82 (137)
Oct. 14–21 ...	440	3·94 (153)	Nov. 1– 7	164	3·00 (108)
Oct. 27 to Nov. 1	180	3·90 (151)	Unsprayed	36	2·78 (100)
Unsprayed ...	64	2·58 (100)			
Sowing started ...	August 12th		August 5th		

all sprayed ; in addition the variety was changed. Yields were records except in the case of Dueim, which only had 68 per cent. of its small area of 420 feddans sprayed at a date which was considered too late. Spraying at Wad Nimr was also carried out late, at the end of November, but the yield was excellent ; at Fatisa and Hashaba spraying was in October, at Umm Gerr in November. It was quite impossible to assess the relative effects of spraying, variety, manuring and season.

In 1949/50 all schemes were sprayed, again starting in early October, but largely finishing by the end of that month. Yields were again good. Season 1950/51 was outstanding, as in the Gezira ; all cotton was sprayed. If the average yield of the three seasons 1944/45 to 1946/47 of unmanured Sakel, with spraying, are compared against the average yield for manured and sprayed X1730A in the three seasons 1948/49 to 1950/51, the increases at Fatisa, Wad Nimr and Hashaba are much greater than further south at Umm Gerr, mainly, it is suggested, because the Jassid is extremely serious in the north, although appreciable in the south.

Summary.

The damage caused by the Cotton Jassid to the Egyptian-type cottons in the Gezira and White Nile areas of the Sudan is very considerable. Realisation of this fact has been greatly aided by chemical control of the pest in small-scale experiments, followed by large-scale work with tractor-drawn sprayers and with helicopters fitted with spraying equipment. This paper deals primarily with examination of available records pertaining to the cotton crops in the four seasons from 1946/47 to 1949/50, preceded *firstly* by an introduction which emphasises the importance of yield records in the appraisal and interpretation of losses from pests, and *secondly* by an account of certain aspects of the pest in the Gezira Scheme.

Large-scale spraying to control the pest started in the Gezira in the crop season 1945/46 ; yield increases from about 1,250 feddans (acres) sprayed with 0·1 per cent. DDT emulsion were very satisfactory. In succeeding seasons increasing areas were sprayed ; in 1947/48 spraying was extended to the cotton farms along the White Nile between Khartoum and Kosti ; in 1949/50 the total area sprayed in the Sudan was over 150,000 feddans. Material and also methods and dates of application varied considerably.

Gezira.

Most spraying was carried out on Domains Sakel cotton with 0·1 per cent. DDT emulsion applied at 100 gallons per feddan (1 lb. DDT per feddan) by tractor-drawn sprayers in October and November.

Of outstanding importance were the variations in yield increase with date of spraying. In 1946/47, 1947/48 and 1948/49 yield was a linear function of the date of spraying, *i.e.*, the earlier the spraying the greater was the response. In 1949/50 there was no significant difference between yield increases at various dates of spraying. On the average, therefore, early spraying was more profitable. Since in general the Jassid population gradually increases during October and November it is inferred that the ultimate effect on yield by one Jassid is often more in October than in November.

Yield increases were good in 1946/47, 1947/48 and 1949/50; in 1948/49 and 1950/51 they were considerably less, although substantial with early spraying in 1948/49. Season 1950/51 awaits full examination.

The above results applied whether the land was unmanured or received nitrogenous manure prior to sowing. Nevertheless there were consistent indications, albeit significant only in one case, that the yield increases attributable to spraying were rather greater in the case of manured land.

Quite considerable areas were sprayed with 0·1 per cent. DDT wettable powder in November; compared with emulsion the differences were not significant, although wettable powder was consistently inferior.

Small areas were sprayed with 0·075 per cent. and 0·05 per cent. DDT emulsion. The yields were slightly less than with 0·1 per cent. DDT; the differences were not significant.

Spraying had no adverse effect on grade of cotton; the increased yields were obtained mainly or entirely in the latest pickings.

Yield increases obtained by application of 1 lb. of DDT emulsion at low volume by helicopters seemed satisfactory, but there were no suitable comparisons with ground application at high volume.

The population of Jassid normally decreases from north to south. Spraying commenced in the north; only by 1949/50 did it embrace all parts of the Gezira, and results in this season showed a decreasing albeit worth-while response from north to south. This was a season of relatively heavy infestation; in 1950/51—a season of lighter infestation—it is likely that there was no response in the extreme south.

It happens that in the south X1730A variety is grown, and in 1949/50 the increase in yield from spraying this variety was greater than from spraying Domains Sakel under comparable conditions.

Increases of over 1 kantar per feddan of seed cotton, *i.e.*, approximately 100 lb. of lint and 200 lb. of seed, were quite common. Since even an extra 1 lb. of high quality lint per feddan over a large area is worth a considerable sum of money, a slight drop or a slight increase in efficiency of spraying is important.

White Nile.

Yields in certain schemes had fallen by 1946/47 to a low level, which was attributed to overcropping during the war. Results from the earlier large-scale spraying in the Gezira drew attention to the potential losses from Jassid in the White Nile cotton. A start with spraying combined with pre-sowing manuring was made in 1947/48. The results were excellent and from 1948 to 1949 it has been the general policy to spray with DDT in this area. Yields are now on a high level.

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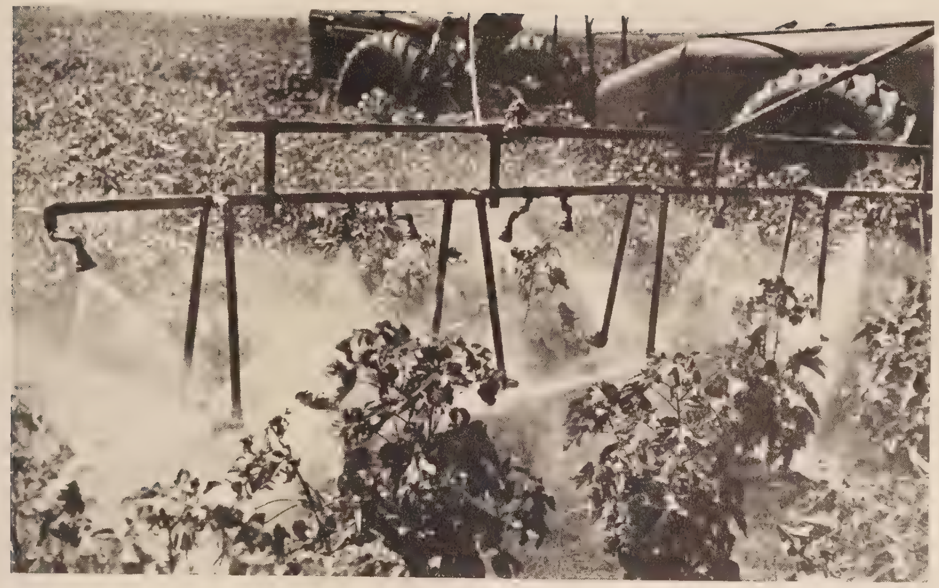

Fig. 1

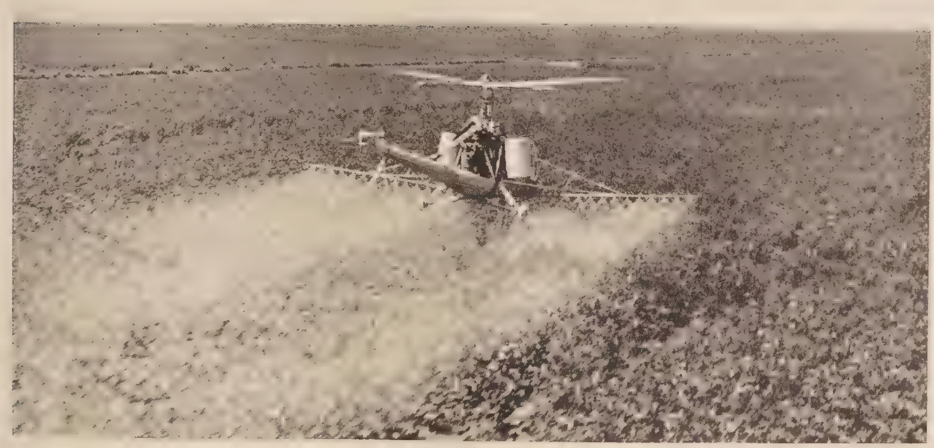

Fig. 2

SPRAYING AGAINST JASSID IN THE SUDAN GEZIRA.

Fig. 1. By tractor drawn power sprayer.

Fig. 2. By Hiller helicopter in season 1950-51.

PARASITES OF THE FRIT-FLY, *OSCINELLA FRIT* (L.), IN EASTERN NORTH AMERICA.

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Although the frit-fly, *Oscinella frit* (L.), is an important pest of oats and other cereals over extensive areas of Europe (Collin, 1918), it is of minor economic importance in North America and has attracted little attention. It was thought possible that this might be due to control by parasites, and an investigation was therefore undertaken with a view to the possible introduction into England of species suitable for the biological control of the pest.

In Europe, some confusion has existed as to the exact specific demarcations between *O. frit* and its close allies. Damage referred to as caused by " frit " is possibly due not to a single species but to a group of closely related species. Moreover, some doubt has been expressed as to whether the North American and European forms referred to as *O. frit* are identical. There appears to be no doubt that the two forms are morphologically identical, though their habits are distinctly different. In Europe, the preferred food-plant of *O. frit* is oats and there is a distinct summer generation attacking the unripe grain in the ear. In North America, the preferred food-plant is wheat and there is no ear-infesting generation (Aldrich, 1920).

Literature on the frit-fly in Europe is extensive, reflecting the importance of it as a pest ; in North America, little has been recorded about it. Garman (1890) records *O. variabilis* (Loew) as damaging wheat in Kentucky in 1889. Fletcher (1891) reports extensive damage by the same species in Canada. Lugger (1896) states that in 1892 farmers complained of serious reduction in their crops due to *O. soror* (Macq.) in Minnesota. Webster (1903) records a bad outbreak of *O. carbonaria* (Loew) in a wheat field near Wooster, Ohio, in 1891, and also further material obtained in Illinois, Indiana, and Ohio. He makes a comparison between this species and *O. soror*, and puts forward suggestions as to measures to prevent outbreaks. Tucker (1911) mentions having reared *O. carbonaria* from green corn-stalks in August at Alexandria, La. Criddle (1913) records extensive injury to spring wheat in Manitoba caused by *O. carbonaria* ; some fields were definitely patchy in appearance, and in parts, 50 per cent. of the plants had been killed. In June and July, a second generation appeared, and larvae and puparia were plentiful at the bases of the plants. A third generation appeared later.

Aldrich (1920) discussed various aspects of the status of the frit-fly in North America, and his is the only paper dealing at all fully with its biology. He is the only American author to refer to attack by frit on the young grain in the ear. He apparently obtained no such attack on wheat. From at least 79,000 kernels of oats he obtained three frit-flies. This contrasts sharply with the condition prevailing in England and Europe where a summer generation infesting the young ears of oats is of regular occurrence. He mentions the fact that " *Oscinis frit* appears to be freely parasitised by minute Hymenoptera ", but gives no details.

Wilbur and Sabrosky (1936) investigated the Chloropid populations on pasture grasses in Kansas and came to the conclusion that there was a definite correlation between adult emergence and rainfall, emergence occurring immediately after a rainy period (*cf.* Cunliffe, 1924, 1925).

That the fly is fairly widespread was also ascertained from correspondence. *O. frit*, *O. carbonaria* and *O. minor* (Adams) were mentioned from Kansas (R. O.

Painter), *O. frit* from Pennsylvania and Maryland (C. C. Hill) and *O. frit*, *O. carbonaria* and *O. soror* from Michigan (C. W. Sabrosky).

The greater part of the present investigation was carried out at Belleville, Ontario, Canada. A brief description of the climate may be useful for comparison with that of the various parts of Europe where detailed investigations of the frit-fly have been made. The monthly mean maximum and minimum temperatures in 1941–1944 were 82·4°F. and 3·3°F., respectively, giving a range of 79·1°F. The snowfall ranged between 42½ ins. and 79 ins. per year and the additional annual rainfall was about 30 ins. In general, the winters are long and severe, snow often lasting until the end of March, and summers are hot and dry ; autumn is long and spring short, the transition from winter to summer being abrupt.

There are numerous wheat, oats, rye and barley fields around Belleville, together with a great deal of market gardening, scattered apple orchards, and large expanses of very rough pasture and forest, mostly conifers, birch, maple, elm and oak. Some of the wheat and all of the oats are spring sown, but most of the wheat is sown in autumn. The farms are small, and there are no such vast areas under one crop as occur in Western Canada ; in this respect, this part of the country is similar to England.

The influence that these differences in climate might have on the frit-fly and its parasites will be discussed later in connection with its general life-history.

The Frit-Fly.

Systematics and Synonymy.

The frit-fly, *Oscinella frit*, is one of the Acalypterate Diptera belonging to the family CHLOROPIDAE. It was first mentioned by Linnaeus in 1750 when he described damage done to young barley grains in Sweden by the larvae of a fly which, in 1758 he named *Musca frit*, the attacked grain being called " frits " in Swedish. In 1805, Fabricius placed the species in the genus *Oscinis* of Latreille (1804), the type genus of the family OSCINIDAE. However, *Oscinis* was found to be a synonym of *Chlorops* Meigen (1803) and is no longer a valid name, and therefore the family name OSCINIDAE was dropped in favour of CHLOROPIDAE. In 1912, Becker formed the genus *Oscinella* for the type species, *O. deficiens*, from North Africa, and doubt has been expressed as to whether *frit* is congeneric with this species. However, until this matter is investigated further, the genus *Oscinella* is still used as intended by Becker for *Oscinis* of authors (nec Latreille).

In the CHLOROPIDAE, the two genera, *Oscinella* Becker (=*Oscinis* auctt. nec Latr., *Oscinosoma* Enderlein, *Botanobia* Lioy) and *Madiza* Fall. (=*Siphonella* Macq.), form a group and are difficult to separate. In general, *Madiza* may be separated by the elongate geniculate proboscis. In *Oscinella*, the vibrissal angle is not produced, the face in profile is vertical or receding, and the oral opening is approximately square and broader than long. *O. frit* itself may be distinguished by the following characters : frontal triangle large, nearly touching the eyes at the vertex and reaching the anterior margin of the front ; front black ; cheeks comparatively broad approximately two-thirds to three-quarters the height of the third antennal segment ; the anterior cross-vein usually entering the discal cell distinctly beyond the mid-point. The mesonotum is dull, covered with fine dark-grey pollen.

There has been for a long while in America, as elsewhere, a great deal of confusion in the taxonomy of the Chloropids, and specific determinations of the " frit-fly " have been very inconsistent owing to the variability of the coloration of the species involved, and to the apparent lack of definite specific characters. Add to this the usual difficulties of synonymy, and it does not seem surprising that opinions as to the identity of the species involved in a number of instances have been conflicting.

Aldrich (1920) deals with the synonymy of common American species of the "frit" group and comes to the conclusion that "*Oscinis pusilla, O. nitidissima, O. carbonaria, O. variabilis, O. nigra* Tucker and *O. soror* Macq. are synonyms of *O. frit.*" The more recent work of Sabrosky (1936, 1939, 1940) disagrees with this and recognises *Oscinella frit* (L.) and its variety *nitidissima* (Meigen), *O. soror* (Macq.) and *O. carbonaria* (Lw.), with the possibility that the last two are genetic forms of the same species. The form *pusilla* (Meigen) is included in the species *O. frit* (L.). It is agreed, as stated above, that the North American and European forms are morphologically identical. The present work has to a limited extent confirmed this. Professor Sabrosky pointed out the specific differences to me, and also let me have specimens of these species. These specific differences were quite distinct, and throughout the work no specimens were seen which could not be determined without difficulty. Furthermore, *O. frit* bred true, as did *O. carbonaria.* Unfortunately, attempts to breed *O. soror* were unsuccessful, but the breeding of the other two offers some confirmation of Sabrosky's specific concepts.

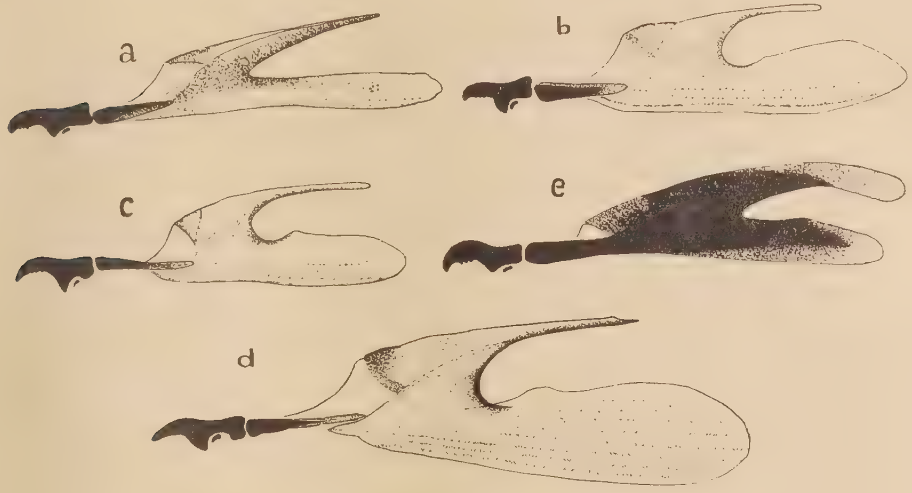


Fig. 1.—Cephalopharyngeal skeletons of species of Chloropids attacking wheat plants. (*a*) *Oscinella frit* (L.) ; (*b*) *O. carbonaria* (Loew) ; (*c*) *O. minor* (Adams) ; (*d*) *Elachiptera costata* (Loew) ; (*e*) *Meromyza americana* Fitch.

In the present work, these three species, together with *O. minor,* are treated as "frit-fly" when percentage parasitism and abundance of the frit-fly are being considered. Other species, such as *Meromyza americana* Fitch and species of *Elachiptera, Madiza,* etc., are excluded from such figures. However, wherever possible the species have been separated in more detailed work. The life-histories of the separate species have never been compared, only that of *O. frit* having been described. During the work in the Eastern United States, other species, *O. umbrosa* (Loew), *O. coxendix* (Fitch), *O. neocoxendix* Sabrosky, *O. flavescens* (Tucker), *Hippelates dissidens* (Tucker) and *H. particeps* (Fitch), were obtained, but only in small numbers, and they were not represented in the material obtained from the wheat plots at Belleville.

In none of the previous work on the frit-fly has any attempt been made to distinguish between the larvae of the several species of *Oscinella* found infesting cereals. Several times the life-history of *O. frit* has been described, and figures of the various stages given (*e.g.*, Steel, 1931). It may be remarked here that the morphology of the mouth-parts of the fully grown larva as described in Steel's paper is in close agreement with that of the American frit-fly, indicating that the similarity between the North American and European forms extends to the larval stages. In the present work, it was necessary, in connection with the specific host relationships of the parasites, to be able to determine specifically host puparia from which parasites had emerged. Puparia from which identified individual Chloropids had emerged were examined. The only reliable character was found to be the cephalopharyngeal skeleton of the fully grown larva which is found adhering to the inner puparial wall at the anterior end of the puparium. The larval mouth-parts of *O. frit*, *O. carbonaria*, *O. minor*, *Elachiptera costata* (Loew) and *Meromyza americana* were examined in this way (fig. 1 and Table I). From these, puparia and empty puparial cases can be identified, as well as fully grown larvae.

Distribution and Food-plants.

The frit-fly has a very extensive distribution across temperate Eurasia and North America, where it has been recorded from the Atlantic to the Pacific and from Alaska to Mexico. The main area in America where it occurs abundantly, according to Aldrich (1920), is " that in which winter wheat is grown from the Great Lakes to the Ohio River, and westward as far as the Missouri ", though the information obtained from correspondence does not indicate that it is abundant all over this area. The range of frit is not determined by the presence of wheat plants, but similar climatic conditions are apparently favourable to both.

Whether the frit-fly has been introduced into North America or was originally holarctic is doubtful, but evidence would seem to favour the latter suggestion. Loew described it, under the name *O. variabilis*, from America in 1863, hence it must have been widespread prior to that date. The distribution of the species over the whole of North America suggests that it has been there for a considerable time, although there is evidence (Hardy & Milne, 1938) that *O. frit* adults may be carried long distances at heights of at least 2,000 feet.

The preference of the American form for wheat as a host plant contrasts with the preference of the European form for oats. The latter form also possesses a definite grain-infesting generation in the summer, a type of attack which does not occur in North America (Aldrich, 1920). This suggests that there are two biological races of the same species. The differences are constant over a wide area and it is extremely improbable that the time available would have sufficed for them to have become so fixed if the fly had been introduced from Europe to America.

Moreover, the parasite complex associated with *O. frit* in America is very similar to that in Europe. Some species are identical, while others, though distinct from European species, have habits very similar to their European counterparts. Such a similarity, without actual identity of all the species concerned, indicates that the host has been established separately in the two areas for a considerable time. Thus the evidence indicates that frit is a holarctic species and that in the course of time it has developed different habits in Europe and America.

Around Belleville, the frit-fly was found to be common throughout the summer, although its abundance varied considerably from field to field. It was not common in sweepings taken over young cereals, was more common in long rough pasture, and most abundant in fields and along roadsides where hay had been cut, this being possibly due merely to the thick cover offered by long grass in rough pasture, which is lost when the grass is cut. In collections of wheat plants made in the field, larvae and puparia were very uncommon, but they were plentiful in experimental plots planted near grass fields. Larvae and puparia were found very uncommonly in young oat plants, and also in the early spring in plants of volunteer rye. Thus, apart from the experimental plots, frit-fly was very rarely found in the larval and puparial stages, although adults were fairly plentiful on the wing in early summer. In no case was there any damage on an economic scale.

In Tennessee in the summer of 1943, *O. frit* was very uncommon, both as larvae and puparia in wheat plants and as adults in sweepings. *O. carbonaria* replaced it to some extent, but this species was not common either. The most common species were *Hippelates* (*Oscinella*) *dissidens* (Tucker), and *H.* (*Oscinella*) *particeps* (Fitch). Further to the north, in the New England States, conditions approached nearer to those in Belleville, but nowhere was frit common in 1943. This may have been due to unusual conditions in 1943, or alternatively, in the south, to the general unsuitability of the climate for frit-fly.

TABLE I.

Characteristics of cephalopharyngeal skeletons of Chloropids attacking wheat plants.

	O. frit	*O. carbonaria*	*O. minor*	*Elachiptera costata*	*Meromyza americana*
Total length of cephalopharyngeal skeleton in mm.	·39	·39	·32	·48	—
Length of mandibular sclerite in mm.	·09	·08	·07	·10	—
Maximum width (ventrodorsal) in mm.	·08	·12	1·0	1·6	—
Chitinisation of hypostomal sclerite	Heavy all over	Lighter at posterior end	Lighter at posterior end	Lighter at posterior end	Heavy all over
Chitinisation of dorsopharyngeal sclerite	Fairly heavy	Fairly heavy	Lighter	Fairly heavy	Heavy
Chitinisation of dorsal prong of pharyngeal sclerite	Heavy	Light	Very light	Light	Very heavy
Chitinisation of ventral lobe of pharyngeal sclerite	Sclerite narrow, rim heavy	Sclerite broad, heavy only near bifurcation with dorsal part	Sclerite broad, heavy only near bifurcation with dorsal part	Sclerite broad, heavy only near bifurcation with dorsal part	Sclerite fairly narrow, very heavy

In 1944, the general survey made in the eastern United States gave further information on the distribution of frit. All species were rare in the south, in Virginia, West Virginia and Kentucky. Further north, in northern Virginia and Maryland, *O. frit* was rare and was replaced in attacks on wheat plants, which were very light, by *Hippelates dissidens* (Tucker), *H. bishoppi* Sabrosky, *O. umbrosa* (Loew), *O. minor* (Adams), *O. neocoxendix* Sabrosky and *O. flavescens* (Tucker). *O. carbonaria* and *O. soror* were observed to replace *O. frit* to a certain extent in areas south of Belleville. Thus the northern parts of this area are more favourable to frit ; further south, there is a gradual replacement of *O. frit* by other forms and the attack is more restricted.

Other plants from which frit-fly has been reared in North America are barley (*Hordeum vulgare*), rye (*Secale cereale*), emmer (*Triticum dicoccum*), maize (*Zea mais*), *Phleum pratense*, *Agropyrum tenerum*, *A. caninum*, *A. repens*, *Elymus canadensis*, *Spartina michauxiana*, *Echinochloa crusgalli*, *Eragrostis minor*, *Cyperus strigosus* and *Veronica novaboracensis*, and also plants of cucumber (*Cucumis sativus*) and of strawberry (*Fragaria* sp.). Wheat plants, having the young shoots attacked, were used exclusively in the present work, except for a very small amount of material obtained from wild grasses.

Life-history.

Very full accounts have been given of the life-history of *Oscinella frit* in Europe, amongst which are those of Collin (1918), Cunliffe (1921), Steel (1931) and Roos (1937). They all agree in essentials but differ with regard to the number of generations in the year, the length of the various stages, and the duration of life and fecundity of the adults. Much of this variation is due to differences in climate where the investigations took place. The life-history in America as described by Aldrich is similar to that in Europe.

Laboratory observations at Belleville were made on flies reared in the laboratory at 75°F., and kept at this temperature, with a relative humidity in the cages of 90–100 per cent. On emergence, adults mated readily, remaining coupled for periods up to half an hour or more. As noted by Aldrich, the behaviour of females with regard to oviposition was very variable. Some laid readily ; others, under apparently identical conditions, did not lay. There seemed to be no definite preoviposition period, and some females began to lay on the day after they emerged.

The conditions under which these rearings were made were similar to those of Aldrich's work. About 20 grains of wheat were sown in flower pots 4½ ins. in diameter, and kept in the greenhouse until the wheat was about 1 in. tall. Then a lantern globe 4½ ins. in diameter at the base was placed over the pot and the joint sealed with thick, gummed, brown paper. The upper end of the globe was covered with fine cheese-cloth supported on a metal frame. The pots were stood in troughs in window ledges and kept well watered. Frit-flies were placed in the jars by means of a sucking tube. When the pots were well watered, tiny globules of moisture appeared at the tips of the leaves (presumably from hydathodes). The flies fed at these globules and apparently no other form of nourishment was necessary. Under these conditions, flies collected in the field lived an average (318 flies) of 12·6 days in the laboratory, with a maximum of 36 days. Of 92 experimental globes set up in this way, 45 produced no progeny, even though the numbers of flies in a globe ranged from single pairs to 40 flies. The greatest number of eggs obtained in a single day was 202 from a globe containing 40 flies. Altogether, from 576 flies contained in 33 of the cages, there were 1,057 progeny, an increase of only 83 per cent., which rendered breeding slow and tedious. This agrees with results obtained by Aldrich. In the first generation of laboratory-bred flies, 99 males and 103 females were used in 15 experimental globes with a varying number per globe. Eight of these produced no flies, and from the other seven there were 132 progeny, from 34 flies.

In order to determine the number of eggs laid by individual females, single pairs *in copula* were placed in globes as above, and the number of progeny in each case noted. Fourteen such globes were started ; in four there were no progeny, and in the remaining 10 there were 1, 1, 2, 3, 3, 4, 6, 10, 18 and 18, respectively. An average here means little, but works out at 6·6 eggs per female in those cages where laying occurred.

Estimates in the literature of the number of eggs laid by a single female are very variable. Rörig (1893) states that 30 is an average figure, Kulagin (1913) gives 20, Wahl (1914) states that 70 may be laid, Aldrich (1920) obtained a maximum of 10 under conditions similar to those in the studies here described, and Roos (1937) states that between 36 and 72 may be laid. Though the maximum number obtained in these breeding experiments was 18, it would thus seem probably that about 30 eggs per female is a reasonable average under field conditions.

After the wheat shoots had been exposed to attack, the globes were taken off the pots and the attacked plants were then kept for (*a*) exposure to parasites, (*b*) dissection of the plants to obtain the frit larvae, or (*c*) left for the emergence of progeny. From the large number of globes in which no eggs were laid it was obvious that conditions were not very satisfactory for oviposition. Several other types of cage were tried, including large trays containing young wheat plants enclosed in cages having cheese-cloth sides and glass tops. None of these, however, proved as satisfactory as the globes, which were therefore retained.

Descriptions of the small, white, elongate eggs have been given by Aldrich (1920), Steel (1931), and others. They were laid on any part of the plant, but the majority were on the lower part of the stem, and many were beneath the tip of the coleoptile sheath ; often there were 10 or more per plant. They are very susceptible to desiccation, and seem to be laid in positions protecting them from this.

The length of the egg stage is variable even under controlled conditions. At 75°F., and 100 per cent. R.H., under which conditions 78·3 per cent. of 303 eggs hatched, most of them hatched on the fifth day though some took as long as seven days. The first-stage larva has been described many times. It bores into the stem, or between the tissue layers of the leaf, and makes its way to the lower part of the shoot. It eats the centre of the stem, causing the shoot to wilt and die.

The larva passes through three stages, according to Steel (1931) and Roos (1937), before pupation occurs. The length of larval life in the laboratory at 75°F. is about 18 days, with wide limits of variation. The larvae are characterised by the structure and size of the mouth-parts and spiracles.

When fully fed, the larva becomes motionless and forms a puparium with two pairs of characteristic projections, at the anterior and posterior ends, formed by the larval spiracles. The outlines of the pupa are easily visible in the puparium. After a few days, the pupa begins to darken and the bristles become apparent. In about 9–10 days the adult emerges, leaving the empty pupal case with a clean horizontal split across the anterior end. Thus the total development time at 75°F. is about 4–5 weeks.

From examination of the stems in which the larvae have been feeding, it has been definitely decided that *O. soror*, *O. carbonaria* and *O. minor* have life-histories similar to that of *O. frit*, and that the damage they cause is similar.

Number of Generations a Year.

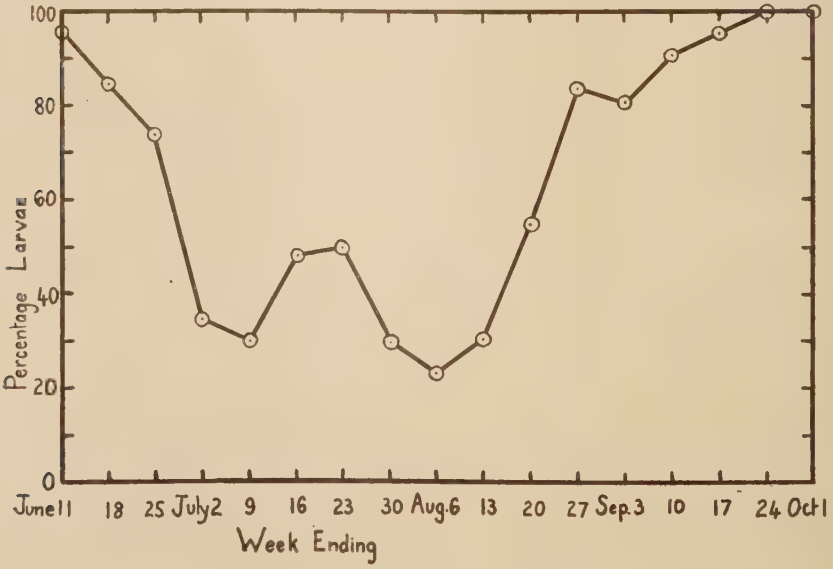
As in Europe, the frit-fly overwinters in the larval stage within the stems of grasses and autumn-sown and volunteer cereals. These larvae form puparia in the early spring from which adults emerge later. In 1942, the first individual of *O. frit* taken in the field at Belleville was obtained on 9th May, although *O. coxendix* was taken on 6th May and *O. soror* on 8th May. From then onwards, adult frit were common in the field for some weeks. In 1943, *O. coxendix* was first taken on 12th May, and *O. frit* on 19th May, a week to ten days later than in 1942. In 1944, *O. frit* was first obtained on 6th May. Also, in 1942, *O. frit* was emerging from volunteer rye near Belleville on 11th May, when the rye was collected, and continued to do so in the laboratory (at 75°F.) until 1st June.

TABLE II.

Percentages of larvae and puparia in total frit material obtained each week in 1942 from laboratory garden, Belleville, Ontario.

Date		No. of larvae	No. of pupae	Percentage larvae
June	11–17 ...	116	6	95·1
	18–24 ...	110	20	84·6
	25– 1 ...	184	62	74·2
July	2– 8 ...	166	309	34·9
	9–15 ...	66	152	30·3
	16–22 ...	118	144	48·5
	23–29 ...	122	123	49·8
	30– 5 ...	207	468	29·8
August	6–12 ...	206	669	23·5
	13–19 ...	205	463	30·7
	20–26 ...	134	106	55·6
	27– 2 ...	46	9	83·6
September	3– 9 ...	97	23	80·8
	10–16 ...	243	26	90·7
	17–23 ...	42	2	95·6
	24–30 ...	6	—	100·0

Thus in 1942, the adults from the overwintered generation emerged over a period extending from the end of the first week in May to the beginning of June. These gave rise to flies of the first summer generation, of which the first record was



Graph 1.

27th June. From the adults obtained from larvae and puparia dissected out from wheat plants throughout the summer it was evident that this first summer generation continued to emerge long after 27th June, until the end of July. This generation was far more numerous than the generation from overwintered larvae. That the month of June came between two peaks of emergence of frit-fly in 1942 is indicated by the ratios of larvae to puparia collected (Table II and Graph I) ; the ratio of the numbers of larvae to puparia is high, and little emergence occurred. From the beginning of August until about the middle of the month, this ratio became lower again, indicating that the peak of the second summer generation of flies was at about the middle of August. This generation was, however, very extended, owing partly to the long period of emergence of the previous generation. From mid-August the ratio of larvae to puparia steadily increased, indicating that there was no further definite generation of adults. The adults of the second summer generation began to emerge at the beginning of August, and some at least of these would give progeny in early September, before the completion of emergence of that generation, since the temperature prevailing in August and September is such that the life-cycle of *O. frit* would cover 4–5 weeks. The last adult emerged on 14th October. These observations apply to 1942, but in 1944 the same general trends were noted, with differences owing to variation in temperature, etc. In 1943, as stated above, there was little frit attack throughout the summer and the data obtained were comparatively valueless. The second generation does not reach the proportions that might be expected from the possible potential increase, and this is undoubtedly partly due to parasite activity.

The numbers and relative abundance of the flies of the different generations in Canada parallel extremely closely the results obtained by Cunliffe (1924, 1925) in his work on the seasonal variation of frit population in England ; his results were derived from the numbers of adults taken in sweepings. The dates of peaks of abundance in Canada correspond surprisingly closely with those obtained in England, in spite of the differences in climate between the two countries.

A detailed examination of meteorological data for Belleville failed to show any correlation between peaks of emergence and periods of high rainfall as was suggested by Wilbur and Sabrosky (1936) for Chloropid populations in Kansas (where different climatic conditions may cause different results). This again agrees with the findings of Cunliffe, who failed to obtain a correlation between dates of maximum abundance of frit and meteorological conditions in England ; he was, in fact, impressed by the regularity of these peaks over a number of years in spite of varying meteorological conditions.

The only correlation found in the present investigation concerns the time of emergence of the overwintered generation ; a cold, wet spring in 1943 retarded emergence, and was also possibly the cause of the low incidence of frit attack throughout the summer.

Varietal Differences in Susceptibility to Frit Attack.

In England, the susceptibility to frit attack shown by various varieties of oats has been investigated by MacDougall (1912) and Cunliffe & Fryer (1924, 1925), and definite differences have been found. Similar trials were made in Canada with different wheat varieties. Five series of samples were taken from plots of a number of varieties throughout the " frit season " in 1944. Some difference in susceptibility was observed, but it would appear that subsequent parasite attack on frit is similar in all varieties.

Parasites.

General.

All the parasites reared were Hymenoptera. A number of adult frit were dissected and examined under the microscope, but no Nematodes, such as *Tylenchinema*

TABLE III.

	England	Germany	Russia	Switzerland	Bulgaria	Poland	Italy
Chalcidoidea							
MISCOGASTERIDAE							
Halticoptera fuscicornis (Wlk.)	×						
Halticoptera petiolata Thoms.		×	×				
Halticoptera suilius (Wlk.) (may be same as *H. fuscicornis*)		×					
Halticoptera aenea (Wlk.)		×	×	×			
Semiotellus nigripes Lind.		×	×				
PTEROMALIDAE							
Callitula bicolor Spin.	×	×	×	×	×		
Callitula pyrrhogaster (Wlk.) (possibly a form of *C. bicolor*)	×						
Cyrtogaster vulgaris Wlk.		×					
Eupteromalus micropterus (Lind.)			×				
Habrocytus sp.		×					
Merisus intermedius Lind.		×	×				
Merisus destructor (Say)			×				
Polycystus oscinidis Kurdj.		×	×				
Pteromalus puparum (L.)		×	×				
Pteromalus planiscuta Thoms.			×				
Spalangia fuscipes Nees			×				
Spalangia sp. (? *nigra* Latr.)		×					
Stenomalus micans (Ol.)		×	×				
Trichomalus cristatus (Först.)		×	×	×			
Trichomalus frontalis Thoms.							
EULOPHIDAE							
Neochrysocharis immaculatus Kurdj.		×	×			×	
Neochrysocharis albiceps Kurdj.			×				
Pleurotropis metallicus (Nees)			×				
MYMARIDAE							
Gonatocerus sulphuripes (Först.)		×					
Ichneumonoidea							
BRACONIDAE							
Aphidius granarius Marsh.	×						
Chasmodon apterus (Nees)	×	×	×				
Dacnusa tristis (Nees)			×				
Gyrocampa pospelovi Kurdj.		×	×				
Sigalphus caudatus Nees	×		×				×
Proctotrupoidea							
DIAPRIIDAE							
Ashmeadopria sp.		×					
Ashmeadopria variipes (Kieff.)			×				
Loxotropa tritoma (Thoms.)	×	×	×	×			
Cynipoidea							
FIGITIDAE							
Cothonaspis (subgen. *Hexaplasta hexatoma* (Först.)		×		×			
Eucoila (subgen. *Rhoptromeris*) *eucera* (Htg.)	×	×	×	×	×		
Eucoila (subgen. *Rhoptromeris*) *eucera* var. *tristis* (Htg.)		×					
Pseudeucoila sp.		×					
Psichacra sp.	×						

oscinellae Goodey (Goodey, 1930), were found. These parasites cause total or partial sterility in the adults and might be important in biological control.

The parasite species recorded from the frit-fly are numerous, but in many cases the records are doubtful. Those given in the Parasite Catalogue of the Commonwealth Institute of Biological Control are listed below, together with the countries from which they have been recorded. It is noteworthy that all the records are European, and that there is no record from the American continent.

Webster (1903) states that he reared *Cyrtogaster occidentalis* Ashm. from a species of *Oscinis* in Indiana. Aldrich (1920) reared a number of parasites but could not be certain that they came from frit material.

In the present investigations, the following parasite species were reared from *O. frit* :—

- Chalcidoidea
    - PTEROMALIDAE
        - *Callitula bicolor* Spin.
        - *Polyscelis* sp. n.
        - *Spalangia drosophilae* Ashm.
- Proctotrupoidea
    - DIAPRIIDAE
        - *Loxotropa* sp.
- Cynipoidea
    - FIGITIDAE
        - *Hexacola* sp. n.
        - *Rhoptromeris* sp.

Another species that was successfully bred on frit puparia was *Cyrtogaster* sp. (probably a new species) but this was not reared from field-collected material.

Regarding the Diapriid, *Loxotropa* sp., it seems almost certain that this is *Loxotropa tritoma* (Thoms.), a species already parasitising frit puparia in England (Imms, 1930). Dr. A. D. Imms sent me a specimen of *L. tritoma* from English frit material, which appeared identical with the species reared here.

However, Dr. C. F. W. Muesebeck writes : " It is possible that these are *tritoma* Thomson, as they have been identified by Simmonds, but I cannot be sure. The original description is inadequate, and without authentic European material for comparison that identification is not safe. They do not agree with European specimens in the National Museum that are labelled *tritoma.* The single Diapriid from the British Museum (the one sent by Dr. Imms) labelled *Loxotropa tritoma* seems to be co-specific with American material from the frit-fly ; but I am not at all sure that it is the true *tritoma* of Thomson. I doubt that anyone has compared the frit-fly parasite with Thomson's type, and in that case the identification must be considered largely a guess, for Thomson's specimens were not recorded from the frit-fly and his description would fit even better the entirely different species in the National Museum that has been identified as *tritoma.*"

Dr. Imms also sent specimens of *Rhoptromeris eucera* (Htg.), which he had reared from English frit puparia and which had been identified by Hedicke in Berlin. Though it is similar to Cynipids reared in large numbers from frit material in the course of the present investigation, the American material proved to be *Hexacola* sp. and another species of *Rhoptromeris.* Mr. L. H. Weld said of the former : " They agree with a species of *Hexacola* captured on flowers of parsnip in June at East Falls

Church, Va. They do not agree with the description of *H. hexatoma* Thoms., Europe, or *H. californica* Kieffer, California, the only species described in the genus so far as I know."

The relative abundance of these species will be discussed elsewhere. Here, details of the biology of each species will be given. In all cases only a single parasite emerged from each puparium.

The material used was dissected from infested wheat plants. It has been shown above that collections of wheat plants from fields in the early spring yielded no frit material, nor could any damage be found in the field. However, Aldrich states that heavier infestations than could be found in the field were obtained by planting wheat in gardens, and therefore rows of wheat were planted in the laboratory garden from early May 1942, at irregular intervals throughout the summer as earlier rows were exhausted. There is at one side of the garden a field of rough grass which it was thought might act as a reservoir for both frit-flies and parasites. Later, to obtain further results from different localities, similar rows of wheat were planted elsewhere, again beside rough grass fields ; these were on two farms, one about 10 miles north-east of Belleville, the other 10 miles south of the town.

In the early part of the summer (*i.e.* the first three weeks in June), these plots were examined, and shoots that had been attacked were taken into the laboratory for dissection and examination. Later, when the infestations became heavier, the wheat was removed from the field without examination, and all of it was dissected under the binocular in the laboratory, each shoot being carefully examined for puparia lying beneath ensheathing leaves ; the shoot itself was then cut up with a needle and examined for larvae.

Puparia obtained in this way were placed individually in small glass vials measuring 1½ ins. × ¼ in., the mouths of which were then plugged with water-soaked cotton wool. The vials were left in racks at 75°F. until the hosts and parasites emerged. The racks were periodically watered to keep the cotton-wool plugs moist. Each day, the vials were examined and the insects that had emerged from each collection recorded, those from larvae and puparia being kept separate. The totals for each collection were recorded when all living material had emerged. Empty puparia were also recorded for the purpose of estimation of populations. Larvae were placed individually in sections of young wheat stems 1 in. long, which were kept in vials plugged with soaked cotton wool, and the insects that emerged were noted as before. Thus throughout the summer, a record was obtained of the number of full-grown larvae and puparia in each collection, together with the number of empty puparia associated with them and the numbers and species of frit and parasites that emerged from the larvae and puparia collected.

Prior to finding parasite material in this way, and when it seemed doubtful if any such infestation of the wheat plants would occur, two other methods of obtaining parasites were tried.

Pots of young wheat plants bearing frit-fly eggs were placed in rough grass fields, left for five days, and brought back to the laboratory before hatching. The resulting larvae were kept in grass stems in the laboratory, but no parasitism had occurred. Other similar pots containing young frit larvae exposed to possible parasitism gave negative results, with the exception of one example of *Hexacola* sp.

In the second method, a number of minute Hymenoptera were obtained with frit-flies by sweeping over grass pastures. It seemed possible that some of these might be frit-fly parasites, and in view of the negative results obtained in the efforts to find parasitised material in the field at the beginning of the season, it was thought worth while attempting to ascertain if any of these parasites would attack frit material in the laboratory. In three experiments, several possible egg parasites of frit were placed with frit eggs, in each case with negative results, no interest being shown in the eggs by the parasites. In three other experiments, a miscellaneous collection of small Hymenoptera was placed in globes with wheat plants containing all stages of frit. These also gave negative results, although plenty of adult frit-flies emerged. In 20 other experiments, parasites collected in the field were placed, either singly or several species together, with a number of unparasitised frit-fly puparia. In only four instances did parasitism take place ; in two of these the species involved was *Spalangia drosophilae* Ashm., in the third *Callitula bicolor* Spin. and in the fourth *Cyrtogaster* sp.

This method produced three parasite species that would attack frit puparia in the laboratory, but it did not show whether they were common frit-fly parasites in the field. The results obtained were therefore not entirely satisfactory, and the use of the method was discontinued when it became apparent that frit material collected in the field was parasitised to a high degree.

Life-histories of the Parasites.

The two larval parasites are dealt with first.

(a) *Hexacola* sp. n.

As stated above, the specific determination of the species of Cynipids reared from frit is doubtful and it would seem probable that this material consists of one or two new species (fig. 2). The species belong to the Eucoiline division of the Cynipid family FIGITIDAE, and are closely related to the European frit-fly parasites, *Cothonaspis* (subgen. *Hexaplasta*) *hexatoma* (Först.) (not synonymous with *Hexacola hexatoma* (Thoms.)) and *Eucoila* (subgen. *Rhoptromeris*) *eucera* (Htg.). The species differ from *Rhoptromeris*, a parasite already found on frit-fly in England, in having an open, not closed, radial cell, and the third, not fourth, antennal joint of the male elongated ; the first abscissa of the radius is straight, not bent, and the disc of the scutellum is straighter than in *Rhoptromeris*. A species of *Rhoptromeris* itself has also appeared from frit material in very small numbers, but has not been further investigated.

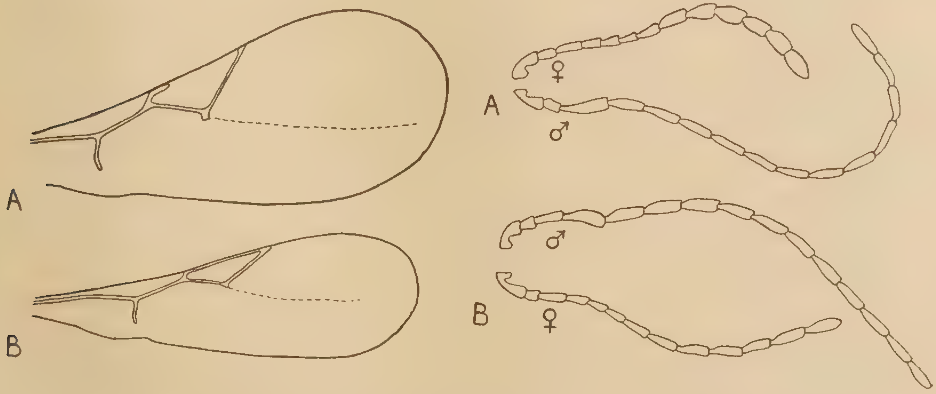


Fig. 2.—Differences between wings and antennae of (A) *Hexacola* sp. n. and those of (B) *Rhoptromeris* sp.

There are no host records for *Hexacola* in the Parasite Catalogue of the Commonwealth Institute of Biological Control, but *Rhoptromeris* and other Eucoilines are characteristic parasites of small cyclorrhaphous dipterous larvae, and a host list of this and other related species is given by Imms (1930). From the frit-fly parasite list given above it is seen that several related species are parasites of the frit-fly in Europe. The life-history of a related form, *Cothonaspis rapae* (Westw.), a parasite of *Hylemyia brassicae* (Bouché), has been described by James (1928).

Like its close relative, *Rhoptromeris*, in Europe, *Hexacola* is one of the most important frit-fly parasites in the neighbourhood of Belleville, reaching a parasitism of 54·4 per cent. of the frit-fly larvae collected between late July and the end of August 1942. Altogether, in 1942, 850 specimens of this species were reared from frit material taken in the field, more than the total of all the other parasites put together. Of these, there were 351 males and 465 females, indicating a sex ratio of 57 females to 43 males.

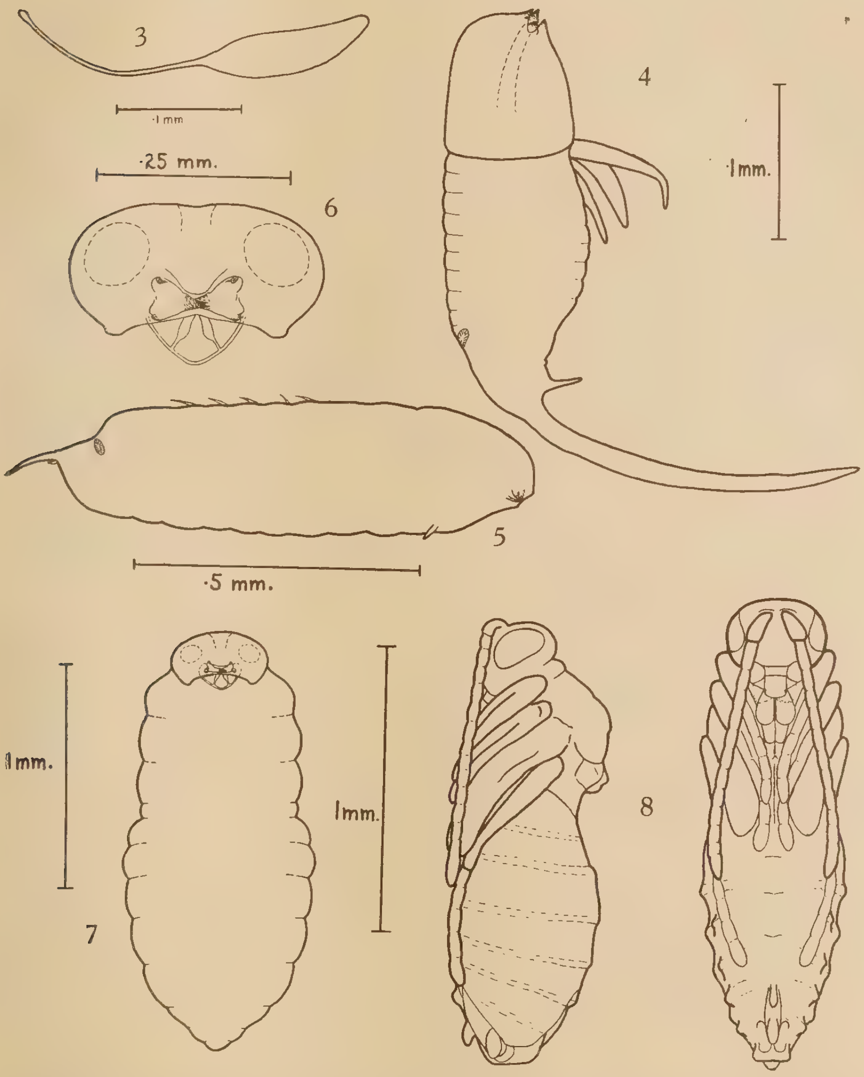
Hexacola was bred in the laboratory, but not so easily as the other species because it parasitises larvae, which are more difficult to deal with experimentally than puparia, and also because for the greater part of the time only field-collected larvae were available and these had already been subjected to considerable parasitism by *Hexacola*, so that results were uncertain.

Mating occurred readily upon emergence and was without any particular point of interest except that the ovipositor was extended while it was in progress. The male approached the female with wings vibrating, stroking the female's antennae with its own for some time prior to copulation, which was very brief. For oviposition, mated females were placed in vials similar to those used for *Callitula* (see p. 529) but with the frit puparia replaced by inch lengths of young wheat stems in which full-grown frit larvae had been placed the previous day. The females showed great interest in these stems, tapping with their antennae along their entire length. When a female found itself over the spot at which a larva was situated, the antennal examination became more pronounced and the insect walked back and forth over the spot several times. Eventually, the ovipositor was unsheathed and forced through the plant tissues into the larva below, the egg being laid in the host, which was not paralysed. After exposure to parasitism, each piece of stem was kept separately in a vial plugged with wet cotton wool for further developmental studies of host and parasite.

Hexacola females showed no interest in either eggs or puparia of frit. Whether young larvae as well as full-grown ones are attacked is not known, but one experiment indicated that they are probably suitable for attack. Females were also offered larvae of *Drosophila melanogaster* in various stages, both free and placed in different ways in pieces of wheat stem, filter paper soaked in a grass infusion, etc. In a few cases some interest was shown, and stabbing movements were made, but no parasite eggs or larvae were found on dissection, nor were any progeny reared.

Although a search was made for eggs within frit larvae, none was found. Eggs were, however, dissected from the oviducts of the female (fig. 3). They are of the stalked type common in Cynipids, and resemble those of *Cothonaspis rapae*, of which the period of incubation is about six days.

The primary larva is shown in fig. 4. It is eucoiliform in shape, about 0·5 mm. long and 0·1 mm. in width. About two-fifths of the length of the body is composed of a slender cauda, and there are three pairs of slender thoracic appendages about 0·06 mm. in length. The head is distinct, and has at the anterior end an oval opening raised on a slight projection. There are also chitinous structures, though definite mandibles could not be distinguished. The head capsule is well demarcated from the rest of the body. There follow three thoracic segments bearing the appendages mentioned, followed by an indistinctly 7-segmented abdomen and the long cauda, which has spine-like projections at the distal end. The anus is situated dorsally at the posterior end of the abdomen, and posteriorly and ventrally to it, at the anterior margin of the tail, is a pointed projection (a feature of eucoiliform larvae). No tracheal or spiracular system was observed.



Figs. 3–8.—*Hexacola* sp. n. ; (3) egg ; (4) first-stage larva ; (5) larva eight days old ; (6) head capsule of fully grown larva ; (7) prepupa ; (8) female pupa (lateral and ventral view).

The next stage observed is shown in fig. 5, which depicts a larva found within a host eight days after exposure of the host to an ovipositing *Hexacola*. The long tail of the primary larva is now reduced to a mere " horn " at the posterior end, and the larva is now 0·75 mm. long and 0·2 mm. wide. The mouth-parts are indistinct and the head capsule is no longer separated distinctly from the rest of the body. The abdominal segmentation was indistinct in the specimens examined. Dorsally, between the segments, there are long slender spines. Anteriorly in a ventro-lateral position are paired slender projections, and it is highly probable that these belong to a segmental series such as is usually present in the polypodeiform larvae of Cynipids. As in the primary larva, the anus opens at the dorsal side of the posterior end of the abdomen. Again no tracheal system was observed.

The rate of development of the parasite larva seems to be determined entirely by that of the host, since the parasite larva does not become fully grown until after the formation of the host puparium. The early larval stages of the parasite cannot interfere to any great extent with the physiology of the host, since normal puparium formation occurs. If conditions are such as to delay puparium formation the parasite larva undergoes no further development.

After the host has formed its puparium the parasite larva grows quickly, emerges from the shrunken host and finishes feeding external to the host within the puparial shell. The host remains are pushed to one end of the puparium and the fully grown larva occupies the latter almost entirely. The larva is now stout and cylindrical. It is about 2·0 mm. in length and 0·8 mm. broad. There is a distinct head capsule, with prominent bidentate mandibles which are sclerotised at the tip and at the points of attachment to the cephalic skeleton ; this is peculiar in shape, there being epistoma and pleurostoma with a pair of supporting struts as shown in fig. 6. The head capsule is about 0·3 mm. wide, and at the extreme anterior end are two large swellings. There are eight pairs of spiracles, but further details of the tracheal system have not yet been ascertained.

The fully grown larva becomes motionless and a constriction develops behind the first three segments, separating the thorax from the abdomen. This is the prepupal stage, which is creamy white, about 2·0 mm. in length (fig. 7) and lasts about 24 hours before giving rise to the pupa.

The pupa is much deeper than it is wide (fig. 8). The head is comparatively small, and there is a peculiar projection above the scutellum ; there are also other median projections on the ventral surface of the posterior end of the abdomen of the female pupa. The abdomen, too, has a number of small knob-like projections in two rows on the lateral line. The sex of the pupa can easily be recognised since the antennae of the male are much longer than those of the female and have the third joint considerably elongated. The abdomen of the male is relatively longer than that of the female and lacks the median ventral processes.

The pupa darkens gradually to the dark sepia brown of the adult and after a very variable length of time the adult emerges from a large irregular circular hole bitten through the puparial wall, always (judging from 50 examined) at the anterior end of the puparium, indicating that the parasite pupa is always orientated in the same direction relative to the host puparium.

The length of life of adults placed in vials, with cotton dampened with honey water and with a raisin, and kept at 75°F., was :—

Males	11, 11, 15, 15, 16, 34, 38 days
Females	17, 17, 17, 18, 19, 21, 25, 32, 34, 35, 40 days

or, an average of 20·0 days for the 7 males, and of 25·0 days for the 11 females.

In the laboratory at 75°F., development from oviposition to emergence of the adult occupied between 4 and 5 weeks. However, from material collected in the field somewhat peculiar results were obtained. Table IV gives the times of emergence of *Hexacola* from material collected in the field and brought into the laboratory, the emergences being tabulated in weekly periods.

TABLE IV.

Days after collection...	0–7	8–14	15–21	22–28	29–35	36–42	43–49	50–56	57–63
No. of *Hexacola* emerging from									
(*a*) host material collected in larval stage ...	—	—	11	30	29	20	12	11	1
(*b*) host material collected in puparial stage ...	10	16	65	56	60	161	174	49	2

It is to be expected that no adult parasites would emerge from host material collected as larvae until about 14 days after collection, since puparium-formation and subsequent development of the parasite must occur after collection. The maximum emergence occurs 3–6 weeks after collection, as would be expected from the breeding experiments. However, when the dates of emergence from puparia are considered, it is seen that maximum emergence occurs 5–7 weeks after collection, and this is far longer than would be expected. The only possible explanation is that owing to the change of conditions when the puparia are brought from the field into the laboratory, the development of the parasites is delayed, and that no such delay occurs when development from the larval stage of the host takes place without change of environment. From these figures it is also evident that the period of development is very variable and may be extended to over 8 weeks. Allowing an adult life of 3 weeks, this indicates that adult parasites of one generation can be present over a period of nearly 3 months, or nearly the whole of the frit-fly season.

In 1942, the first *Hexacola* emerged in the laboratory on 9th July from a puparium collected on 23rd June. This and subsequent records show that in 1942 parasitism by *Hexacola* in the field first occurred about the middle of June, and that adults of this generation began to appear in the 2nd week in July. The last emergence occurred on 11th September. This indicates that a spring generation of *Hexacola* emerges about mid-June from overwintered material and that there is a summer generation in mid- and late-July. Owing to the varying length of the developmental period, it is probable that this summer generation extends from mid-July till mid-September, but it seems also that a partial second and even third summer generation results from the early adults of the preceding generation, and that there is a mixture of generations throughout the summer. *Hexacola* adults are, however, present throughout the summer and are able to attain a fairly high degree of parasitism in frit larvae. Similar results were obtained in 1944.

Hexacola is one of the most important frit parasites, but its value as a biological-control agent in England is doubtful, since, as pointed out above, the position it occupies in the American parasite complex is very similar to that occupied in England by *Rhoptromeris*. There would be no risk attached to its introduction, and it might prove to be more efficient than the native British species.

(b) *Polyscelis* sp. n.

This is a new species parasitising frit-fly larvae, and although there is no previous record of it, 190 individuals emerged from the summer collections of material placed in vials in 1942, 9 in 1943, and 179 in 1944. It is thus a fairly common larval parasite. The related species, *Polyscelis modestus* Gahan, has been recorded as a parasite and a hyperparasite of *Mayetiola destructor* (Say) in the U.S.A. and Canada by Myers (1924), Hill and Smith (1931) and Gahan (1933), and in Russia by Nikol'skaya (1937). The life-history of this species has been worked out by Myers (1924) who states briefly that it is a parasite of larvae of *M. destructor*, but may also attack larvae within the puparia. There are no other records for *Polyscelis* in the Parasite Catalogue of the Commonwealth Institute of Biological Control.

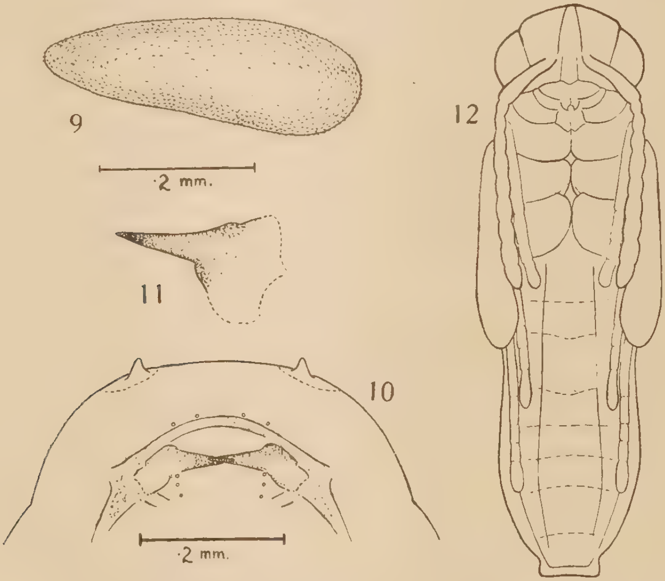
The length of life of adult *Polyscelis* kept in vials with honey-water and a raisin at 75°F. was, in days :—

Males ... ... 1, 4, 6, 8, 12, 12, 17, 18, 19, 19, 28, 31, 35, 35.
Females ... 7, 14, 16, 17, 18, 24, 26, 27, 33, 33, 33, 34, 35, 37.

This gives an average of 17·5 days for the 14 males and one of 25·3 days for the 14 females. For *P. modestus*, Myers (1924) found an average of 9·0 days for the males, and the female life varying from 7 to 39 days.

In the laboratory, females of *Polyscelis* did not attack larvae of either *Oscinella* or *Drosophila*, although both were presented to mated females in a variety of situations, such as sections of wheat, filter paper soaked in an infusion of wheat leaves, etc. Consequently full details of the life-history were not observed. However, some observations were made from field-collected material and a general idea of the various stages was obtained.

The egg, dissected from adult females, is whitish, elongate and curved as shown in fig. 9, about 0·35 mm. in length and 0·15 mm. in width at the widest part. The chorion is closely covered with short blunt protuberances.



Figs. 9–12.—*Polyscelis* sp. n. : (9) egg ; (10) head capsule of third-stage larva ; (11) mandible of third-stage larva ; (12) male pupa, ventral view.

The first-stage larva on hatching is slightly longer than the egg, and is of the cone-shaped type found in a number of Chalcids, being widest at the anterior end. The head has a pair of prominent antennae, and simple sickle-shaped mandibles. There are several lateral setae on each of the first four segments. No spiracles were observed in the specimens examined.

The mature larva within the host puparium, after completely devouring the host, is of the usual stout grub-like form, 13-segmented and tapering towards the posterior end, and is about 1·8 mm. long and 0·5 mm. in width. It is transparent white, with the contents of the mid-gut showing dark through the body wall. The cuticle is smooth and there are lateral rows of fine setae, and also terminal setae at the caudal end. Spiracles were observed on segments 2–10. The head capsule is distinct (fig. 10), bearing a pair of short, brownish antennae each arising from a broad papilla. The mandibles (fig. 11) are almost straight, simple and lightly sclerotised, and are attached to an indistinct head skeleton. There are a number of sensillae around the mouth.

There is a short prepupal stage in which a constriction appears behind the first three segments, separating the thoracic and abdominal regions. The pupal stage lasts about a week. The pupa (fig. 12) is at first white, but darkens to a very dark metallic green in the males and metallic brown in the females, prior to emergence.

From a consideration of records of parasitism, it is evident that *Polyscelis* starts its controlling action on frit larvae somewhat earlier than *Hexacola*, and that the activities of the two species are complementary in that when one is not abundant, the other increases. *Polyscelis* is not as important as *Hexacola* as a larval parasite, and is similar in its habits and life-history to the English species, *Halticoptera fuscicornis* (Wlk.). However, since it increases larval parasitism above that due to *Hexacola*, its introduction into England is desirable, and under different conditions it might be more efficient.

From field-collected larval material placed in vials in 1942, 30 of the 196 parasites that emerged were *Polyscelis* ; this is 15·3 per cent. (or 3·7 per cent. of all the insects that emerged). From puparial material, 160 of 1,381 parasites were *Polyscelis*, and this is 11·6 per cent. (or 5·6 per cent. of all the insects that emerged). In 1943, the total larval material gave a parasitism of only 2·8 per cent. by *Polyscelis*, and puparial parasitism was 0·7 per cent. In 1944, the figures were 6·4 per cent. of the total emergences from larvae and 10·7 per cent. from puparia. Parasitism of puparia reached 8·5 per cent. of the total emergences in mid-July 1942, and in late August and September this percentage rose, the presence of a relatively larger number of parasitised puparia in the field being due, not to increased parasite activity at this period, but to the fact that the parasitised puparia take longer to yield the adult insects than unparasitised ones, and by this time most of the unparasitised material had already yielded adults.

From larval material collected in the field on 11th June 1942, *Polyscelis* emerged on 4th July, and from that collected on 15th June it emerged on 2nd July. These and subsequent collections and emergences indicate that adult *Polyscelis* are on the wing in early June and that the summer generation begins to emerge in early July. Similar results were obtained in 1944, the first summer generation emerging about 10 days earlier than in 1942. It is clear that there must be two summer generations of *Polyscelis*, and therefore three generations per year.

The last adult to emerge in 1942 did so on 28th September from a puparium collected on 16th September. The method of overwintering is unknown, but there is evidence (November 1942) that the insect overwinters either as a full-grown larva within the empty host puparium or else as a first stage larva within the host larva.

(c) *Loxotropa* sp.

As stated above, there is some doubt as to the specific determination of the specimens of this genus reared from frit. The species is not the same as European specimens labelled *tritoma* in the National Museum at Washington, and yet it agrees with English material bred by Imms from frit puparia and identified as *Loxotropa tritoma* (Thoms.).

Owing to this difficulty, no specific name will be ascribed to the species here, but there is reasonable certainty that the species involved is the same as that reared by Imms at Harpenden.

This parasite is a Proctotrupid belonging to the family DIAPRIIDAE. Imms (1930) gives a list of host records, and mentions the occurrence of species of this genus in association with ants' nests, probably as parasites of Dipterous puparia within the nests. Of the host records, Imms says: "Among other records *L. pegomyia* Brues has been reared from *Pegomyia* (*Chortophila*) *brassicae* in Minnesota (Brues 1908). *L. flavipes* Ashm. is mentioned by Bradley (1928) as a hyperparasite bred from cocoons of a Noctuid moth *Papaipema maritima* Edw. [sic=Bird] in New York State, and Kieffer (1916) records *L. helicicola* Kieff. as being reared from a dipterous puparium found in a shell of *Helix aspersa* in France." Meyer (1923), Schander & Meyer (1925), and Riggert (1935) record *Loxotropa tritoma* as a parasite of *O. frit* in Germany; Roos (1937) records it from *O. frit* in Switzerland; Cunliffe, Taylor and Imms (1930) have recorded it from England, and it has also been recorded from *O. frit* in Russia. Imms gives a detailed description of the adults of *L. tritoma* which agrees with that for the species now under consideration.

This insect has not been recorded hitherto as a parasite of *O. frit* in America, where it has been found to be an endoparasite of the pupa, although in one instance it was bred as an endoparasite from larval material.

Loxotropa sp. is an important parasite of frit at Belleville. In numbers, throughout the three seasons, it was third in importance, *Hexacola* and *Polyscelis*, the larval parasites, being obtained in larger numbers. Of 1,381 parasites which emerged from puparia in 1942, 195 were *Loxotropa*; this is 14·1 per cent. of the emerging parasites (5·2 per cent. of the total emergences from puparia). This figure tends to underestimate the importance of *Loxotropa*, since 31·2 per cent. of the emergences from puparia were *Hexacola* and *Polyscelis* so that only 68·8 per cent. of the puparia available to ovipositing *Loxotropa* were unparasitised. This argument holds, of course, for all the pupal parasites. Consequently, the importance of *Loxotropa* in destroying unparasitised puparia is about 50 per cent. greater than is indicated by the figure 5·2 per cent. In 1943, there was no pupal parasitism, and in 1944, *Loxotropa* was by far the most important pupal parasite, parasitising 7·0 per cent. of the total puparia, or 10·0 per cent. of those not already containing larval parasites.

In the figures given by Riggert (1935) for parasitism in Germany, *L. tritoma* is an unimportant parasite; and figures for parasitism in Switzerland given by Roos (1937) show only three *Loxotropa* amongst 1,651 parasites. Imms (1930 and 1932) shows that in England the importance of *Loxotropa* varies from year to year. In 1926 and 1927, it was relatively unimportant as a frit parasite at Harpenden; in 1929 and 1930, however, it comprised nearly 50 per cent. of the total number of parasites. It probably increases its population when parasitism by larval parasites is low, and when, for this reason, the number of unparasitised puparia is large.

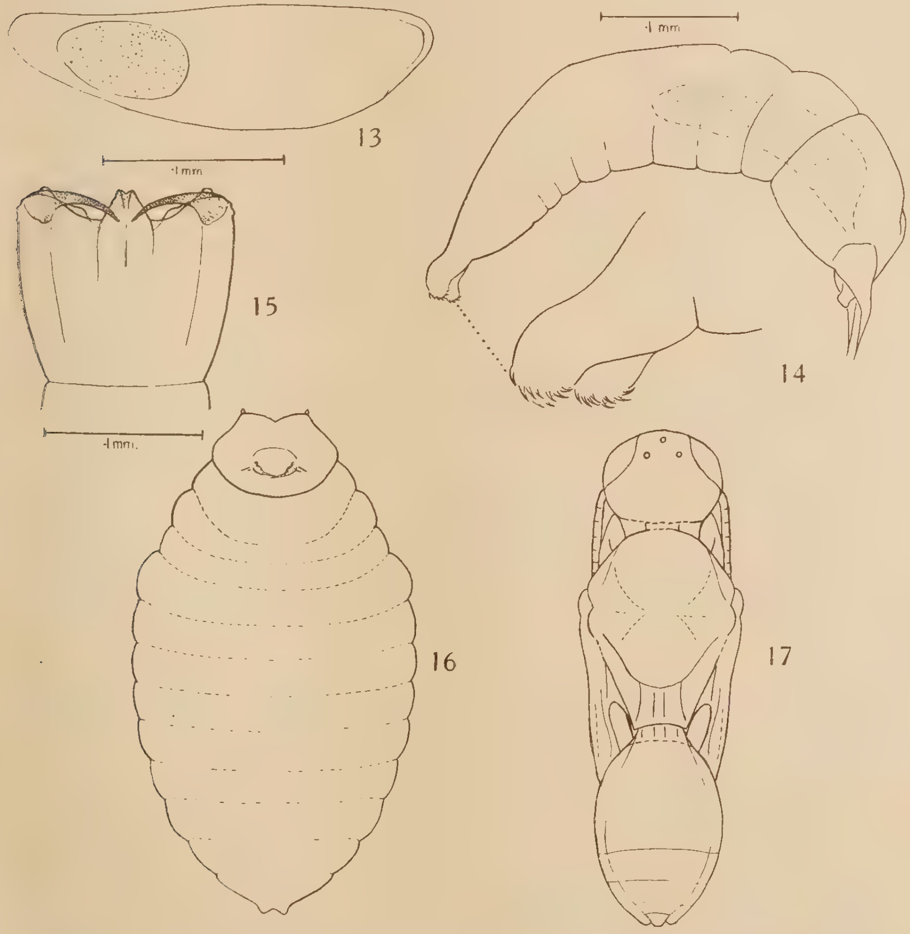
On emergence in the laboratory, males and females mated readily, there being no particular point of interest in the mating behaviour. Females were placed in oviposition vials similar to those used for other pupal parasites and oviposition occurred readily.

The oviposition behaviour, including puncturing, stinging the pupa and feeding at the puncture, is similar to that of *Spalangia* (see p. 533), but the egg is laid, not on the pupal integument, but within the pupa.

Owing to lack of suitable host material it was found impossible to study the life-history of *Loxotropa* with *Oscinella* puparia as hosts. However, the species was reared on *Drosophila* puparia as in the case of *Callitula* and *Spalangia*, and with this host the life-history was worked out.

The egg, shown in fig. 13, is similar in shape to that of *Callitula* but is much smaller, being about 0·25 mm. in length and about 0·07 mm. wide at the widest part. It is translucent-white in colour, and the chorion is unsculptured. At 75°F., the egg hatches in about two days, and the first stage larva begins to feed internally in the body cavity of the pupa. It is of peculiar shape (fig. 14), cylindrical and elongate, about 0·4 mm. in length and 0·1 mm. in width, with a very well marked head region (fig. 15), which bears laterally and anteriorly a pair of papillae which are probably antennae, and a central projection dorsal to the mouth. At the anterior lateral angles are the sickle-shaped mandibles which are devoid of teeth and which are comparatively very large, each extending over half the width of the head. The body, which tapers posteriorily, is indistinctly segmented. There are 9 segments, followed by a caudal region, which ends in a pair of rounded lobes, each bearing ventrally a number of forwardly directed spines.

After about four days, the larva is in the third instar and is fully grown (fig. 16). It is of the usual sac-like form and about 2·0 mm. in length and 0·8 mm. in greatest width. It has a well marked head-region, lightly sclerotised head-skeleton and mandibles, and a pair of papilla-like antennae. The caudal organs of the first-instar larva are represented by a pair of small projections.



Figs. 13–17.—*Loxotropa* sp. : (13) egg ; (14) first-stage larva, lateral view and caudal region of first-stage larva ; (15) head capsule of first-stage larva, ventral view ; (16) third-stage larva, ventral view ; (17) pupa.

The pupa is formed after a brief prepupal stage, when a slight constriction develops behind the first three body segments, demarcating the thorax from the abdomen.

Unlike all the other species of frit parasites, the larva of *Loxotropa* remains within the pupal skin to complete its feeding, and the pupa (fig. 17) is formed within the integument of the host pupa after the contents have been consumed. A very dark meconium is voided on formation of the parasite pupa. A host puparium containing a *Loxotropa* pupa has a characteristic appearance which distinguishes it from those containing any of the other parasites ; it is darker, and the parasite pupa is not visible through the puparial wall.

The pupal stage lasts for about six days, in which time the pupa darkens to the dark brownish-black of the adult. The sex of the pupa can be determined by means of the antennae, which are long and filiform in the male, and short and clubbed in the female.

The adult parasite emerges from the puparium by means of a small, irregularly circular hole bitten through the puparial wall, usually at the anterior end. (Of 100 examined, 98 emerged from the anterior and 2 from the posterior end.)

In the laboratory, host pupae of all ages may be attacked, and many of the parasitised puparia appear to contain the empty integuments of very advanced *Drosophila* pupae.

In one experiment in which *Oscinella* puparia were used as hosts, a single, apparently mated, female was presented with 66 frit puparia between 4th and 23rd August, when it died, 27 days old. No eggs were laid, however, after 15th August, and of the 56 hosts offered to the parasite during its oviposition period, 35 were parasitised, 18 died and 3 produced frit flies. That is, about 52 were parasitised if those that died were parasitised to the same extent as the others. Whether superparasitism occurs was not investigated at this point. In another such experiment, the female lived 24 days and was offered 49 host puparia ; 25 were parasitised, 17 died, and 7 frit emerged, indicating that about 39 of the puparia were parasitised. These figures for the numbers of eggs laid are probably minima, and it is very likely that under natural conditions the numbers are far higher.

The length of life of the adult under laboratory conditions in vials, with honey-water and raisins, was recorded in a few cases. These were :—

Males : 5, 5, 5, 5 days.
Females : 2, 3, 4, 4, 9, 24, 27 days.

The average for the males is 5 days and for the 7 females 10·4 days.

Further details concerning the biology of *Loxotropa* were obtained, as with *Callitula* and *Spalangia*, by the utilisation of *Drosophila* puparia as hosts ; parasites were bred at 70°, 75° and 83°F., at which temperatures the results obtained were as follows :—

TABLE V.

Temperature		Length of life of females in days	Preoviposition period in days	Postoviposition period in days	Total eggs from those females that laid	Sex ratio of progeny from mated females		Developmental period (days)	
						♂	♀	♂	♀
83°F.	Maximum...	19	2	13	25*	—	—	—	—
	Minimum ...	3	—	1	5*	—	—	—	—
	Average ...	12·6	0·1	5·9	16·0*	—	—	—	—
75°F.	Maximum...	40	3	23	86	—	—	28	30
	Minimum ...	13	—	—	2	—	—	21	23
	Average ...	24·5	0·3	12·2	31·4	41·5	58·5	24·01	25·79
70°F.	Maximum...	52	1	39	49	—	—	36	38
	Minimum ...	16	—	—	15	—	—	28	27
	Average ...	38·0	0·1	0·1	38·7	53·8	46·2	30·88	31·83

*No further data are given for 83°F. because at this temperature mortality was extremely high in the pupal stage, only 15 males and 1 female resulted from the 336 eggs laid, and the developmental time of these individuals was abnormal.

(d) *Cyrtogaster* sp.

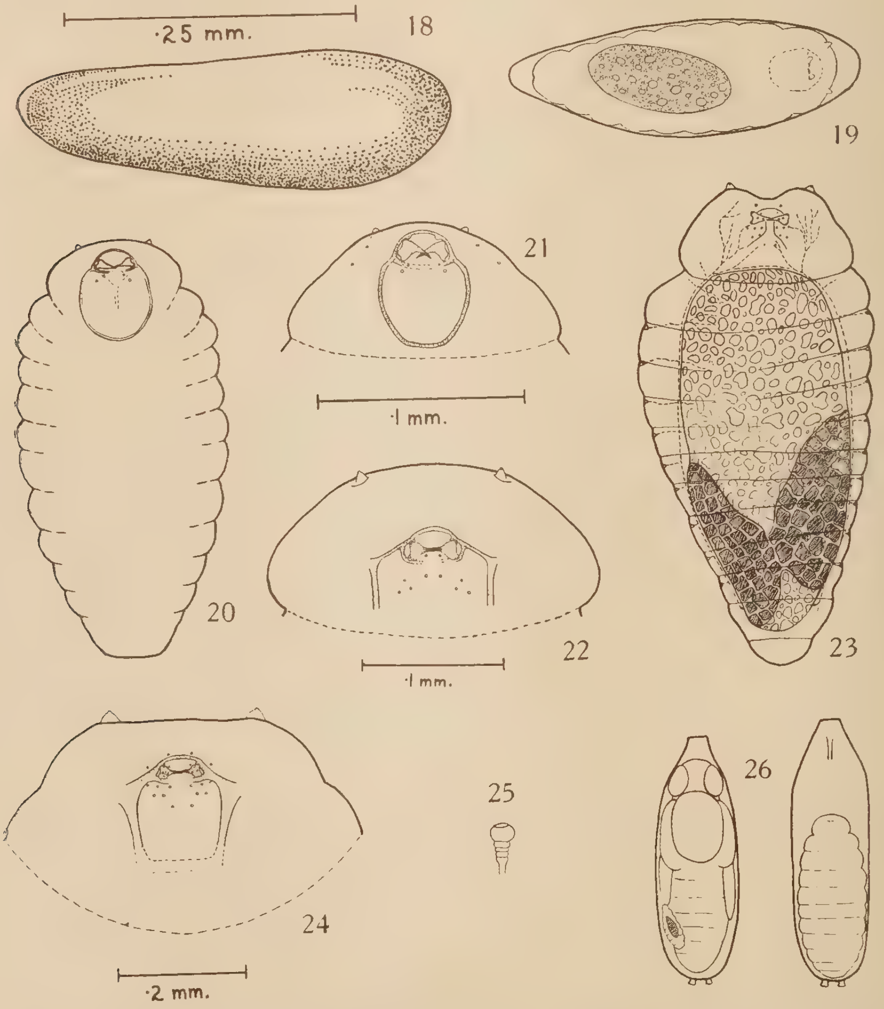
A Chalcid taken in sweepings in the field on 8th July 1942 was placed with frit puparia in a vial as described below for *Callitula bicolor*. Parasitism occurred very readily and progeny were easily reared. This species was identified in Washington as *Cyrtogaster* sp., a Pteromalid of the sub-tribe Sphegigasterini.

This species was never actually reared from field-collected frit material, although a female emerged from a collection of young wheat plants which were heavily infested with frit but also contained other Chloropids and Hessian-fly material. As stated above, Webster (1903) reared *Cyrtogaster occidentalis* from a species of *Oscinis* in Indiana. Dr. Luginbill states that a specimen of *Cyrtogaster liqueatus* Ashm. was reared from Hessian fly material from Lynchburg, Tennessee, and two examples of the same species were reared by Packard in 1931 from north-western Ohio. *C. liqueatus* has also been reared in the U.S.A. from the Agromyzid, *Phytomyza delphiniae* Frost, and *C. occidentalis* from another Agromyzid, *Cerodonta dorsalis* (Lw.). *Cyrtogaster vulgaris* Wlk. was reared in a single instance from a frit-fly puparium by Riggert in Germany in June 1930, and this species is an important parasite of the holly leaf-miner, *Phytomyza ilicis* Curt., in England, whence it has been shipped to Canada. It has also been recorded as a parasite of *Stilpnotia salicis* (L.) in France. *C. glasgowi* Crwf. has been recorded from the Ephydrid, *Brachydeutera argentata* (Wlk.), in the U.S.A.

In all the above cases, *Cyrtogaster* is a primary parasite. There is, however, a doubtful record from Germany of *C. vulgaris* as a secondary parasite through the Braconid, *Coelinius niger* (Nees).

In the present laboratory work, *Cyrtogaster* sp. was bred as a primary parasite of puparia of *O. frit*. A female taken in the field was placed in a vial measuring 4½ ins. ×1 in. and supplied with a raisin and sugar-water. Frit-fly puparia were placed in the vial on a strip of paper, five being put in each day and the previous day's batch of five being removed and labelled (as for *Callitula*) at the same time. The female did not attack frit larvae, but showed immediate interest in puparia, making the usual careful antennal examination, and going backwards and forwards over the length of each. After a minute or less of such examination it unsheathed the ovipositor and proceeded to puncture the puparial wall and the contained pupa, a process occupying about 2 or 3 minutes. The female feeds on fluid exuding from the punctures. Such puncturing may occur several times prior to oviposition. When the parasite is about to oviposit, a puncture is made in a similar way, and an egg is then laid on the frit pupa, usually, as in *Callitula*, in a natural furrow on the surface of the pupa. Punctures in the pupa often show after a while as dark spots. Only one egg is laid on each host as a rule, but superparasitism is fairly common ; in one case 4 eggs were found on one host.

The egg is translucent white, without apparent sculpturing, wider at one end than the other and slightly curved (fig. 18), being 0·37 mm. long and 0·11 mm. wide at its widest point. At 75°F., it hatches in about 24 hours ; of a number under observation, half had hatched in 24 hours (fig. 19).



Figs. 18–26.—*Cyrtogaster* sp. : (18) egg, freshly laid ; (19) egg, just before hatching ; (20) first-stage larva ; (21) head capsule of first-stage larva ; (22) head capsule of second-stage larva ; (23) third-stage larva ; (24) head capsule of third-stage larva ; (25) abdominal spiracle ; (26) relative sizes and positions of first- and third-stage larvae within the host puparium.

The first-stage larva is about 0·4 mm. long and is broadly cone-shaped, tapering slightly to the posterior end. It has a head capsule 0·1 mm. wide which bears a pair of well-developed antennae and has a strong cephalic skeleton (figs. 20 & 21). The first instar lasts from 2 to 3 days.

The second-stage larva is similar to the first-stage but larger, being 0·75 mm. long and 0·23 mm. across the head capsule. The antennae are well defined, and the cephalic skeleton, though broader and longer, is less strongly sclerotised than that of the first stage (fig. 22) ; also there is a greater number of sensoria as shown in the figure. This stage lasts about 2 days, and on an average, ecdysis to the third stage occurs on the sixth day after oviposition.

The third-stage larva (fig. 23), just after ecdysis, is of similar size to the fully grown second-stage ; the head capsule is, however, about 0·5 mm. across, and the cephalic skeleton is larger, though heavy sclerotisation is now restricted to the extremities and the attachment points of the mandibles. There is an increase in the facial sensoria as shown in fig. 24. The larva is translucent white and has a conspicuous brown mid-gut. When fully grown, after 2 days in this stage, it is stout and is about 2·0 mm. in length and 0·9 mm.–1·0 mm. wide at its greatest width, which is at about one-third of its length from the anterior end ; the cuticle is smooth and spineless. On the head there is a pair of prominent two-jointed antennae. There is a well-developed tracheal system as shown in fig. 23, in which no attempt has been made to show all the tracheal branches. There are 9 pairs of spiracles, one of which is illustrated (fig. 25). The relative sizes and positions on the host of the first- and third-stage larvae are shown in fig. 26.

The prepupa differs only in the greater development of the first three segments in comparison with the ten segments of the abdomen. It is similar in size to the fully grown larva. The prepupal stage occurs on the 8th–9th day after oviposition, and lasts about 24 hours.

The pupa (fig. 27) is at first white, but soon begins to darken, and after 5 days the fully developed adult can be seen within the integument. After a pupal period of

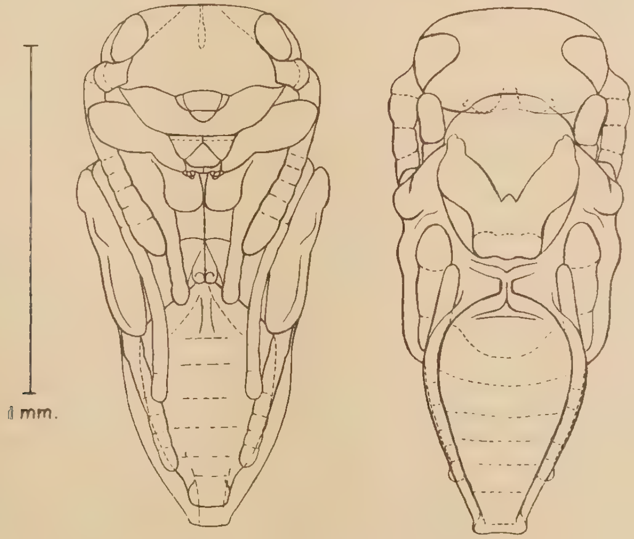


Fig. 27.—*Cyrtogaster* sp. Pupa, ventral and dorsal view.

about 6 days, the adult emerges, biting its way to the exterior through the host puparium. Mating occurs immediately on emergence, the males even tapping with their antennae host puparia from which females are about to emerge. When a virgin female is present, the male approaches, walking with a jerky movement and vibrating its wings. It mounts on to the back of the female, which it clasps round the thorax, and begins stroking the female's antennae with its own. After about 10–15 seconds, the male moves backwards and turns the tip of its abdomen down and under that of the female ; copulation, which lasts about a quarter of a minute, then ensues. Once fertilised, the female resists any further attentions of males.

It was found that the average developmental period of the males is 15·5 days and of the females 16·2 days. The sex-ratio was 60 females : 40 males in the progeny bred. Whether this is the natural sex-ratio in the field is not known.

The original female taken in the field was offered 101 frit puparia, 5 at a time, between 8th July and 23rd August. From these, 5 specimens of *O. frit* and 24 males and 41 females of *Cyrtogaster* emerged ; 18 puparia proved to have been parasitised already and were removed, and 13 were dead. The dead puparia had presumably been parasitised to the same extent as the living material, so that out of 101 puparia offered about 95 were parasitised. Superparasitism occurred, and it is probable that this female laid about 150 eggs in all. A female bred from this parent and mated with a male from the same source was offered 75 puparia similarly between 27th July and 28th August. From these, 2 examples of *O. frit* and 20 males and 26 females of *Cyrtogaster* emerged ; 19 previously parasitised puparia were removed and 8 were dead. Hence, 73 were attacked, and probably over 100 eggs laid.

The length of life of the adults at 75°F. was therefore over 46 days for the original female, and 32 for the other. The length of life of the males was much less than this, being about 10 days, though exact figures were not obtained.

Although this species was not found in the field as a parasite of *O. frit*, it bred on it very readily in the laboratory, laying a large number of eggs. It is possible that if more suitable host species were lacking in the field, parasitism of frit would occur. It would, therefore, be advisable to introduce this species into England with other frit-fly parasites, since change of environment and possible differences in host complex might cause it to attack frit, of which it might become a very efficient natural enemy.

(*e*) *Callitula bicolor* Spin.

The synonymy of this species is dealt with by Imms (1932), and is as follows :—

Callitula bicolor Spin. 1811
Micromelus rufomaculatus Wlk. 1833
Baeotomus rufomaculatus Först. 1856

It belongs to the division Merisinae of the MISCOGASTERIDAE, and has been recorded as a parasite of the Hessian fly, *Mayetiola destructor*, in the U.S.A. and in the Ukraine, where Kurdjumov states that it is always hyperparasitic. Other hosts recorded are *Chlorops taeniopus* Mg. (U.S.S.R.), *Lasiosina cinctipes* (Mg.) (U.S.S.R.), both Chloropids. It has been recorded from *Oscinella frit* in England by Imms (1930), who gives a full description of the adult, and also from the same host in Germany, Bulgaria and Switzerland. Recently, Goodliffe (1942) has reared *Callitula pyrrhogaster* (Wlk.) from puparia of *O. frit* in England, but this parasite may be another form of *C. bicolor* Spin.

During the present work, only 23 specimens were reared from field material in 1942 and 4 in 1944, and it seems that, as in England, it is comparatively rare, being represented in the total year's emergences to the extent of only 0·55 per cent. in 1942 and 0·2 per cent. in 1944. However, specimens collected in the field and others that were reared were utilised in the laboratory for breeding experiments, which were subsequently extended by the use of *Drosophila* puparia as hosts.

Freshly emerged adults placed in a glass vial mated readily. With adults reared from field material, no distinct preoviposition period was noted, but this may depend, as it probably does in many other species of parasites, on the temperature at which the pupae have been kept prior to emergence, a low temperature necessitating a preoviposition period following emergence for the complete maturation of the eggs. In this connection, it is of interest to note some definite observations made in the course of the breeding of *Bracon vulgaris* (Cress.), a Hymenopterous parasite of the larvae of *Loxostege sticticalis* (L.). Adult females that emerged from cocoons kept at 83°F. commenced oviposition on the day of emergence, but those that emerged from cocoons kept at 75°F. required a preoviposition period of from 7 to 10 days.

Mated females of *Callitula* were kept separately in glass vials $4\frac{1}{2}$ ins. long and 1 in. in diameter ; the end of each vial was plugged with a cork covered with muslin, and a wet pad of cotton wool was placed between the muslin and the cork and a raisin pinned to the muslin (fig. 28). A piece of stiff paper was placed so that it fitted into the vial as in the diagram and frit puparia were stuck to the paper with moisture. The cork was removed and dampened each day, being changed when any sign of mould appeared. The parasites were kept at 75°F.

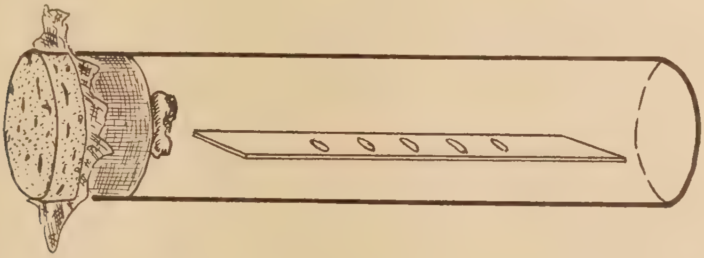
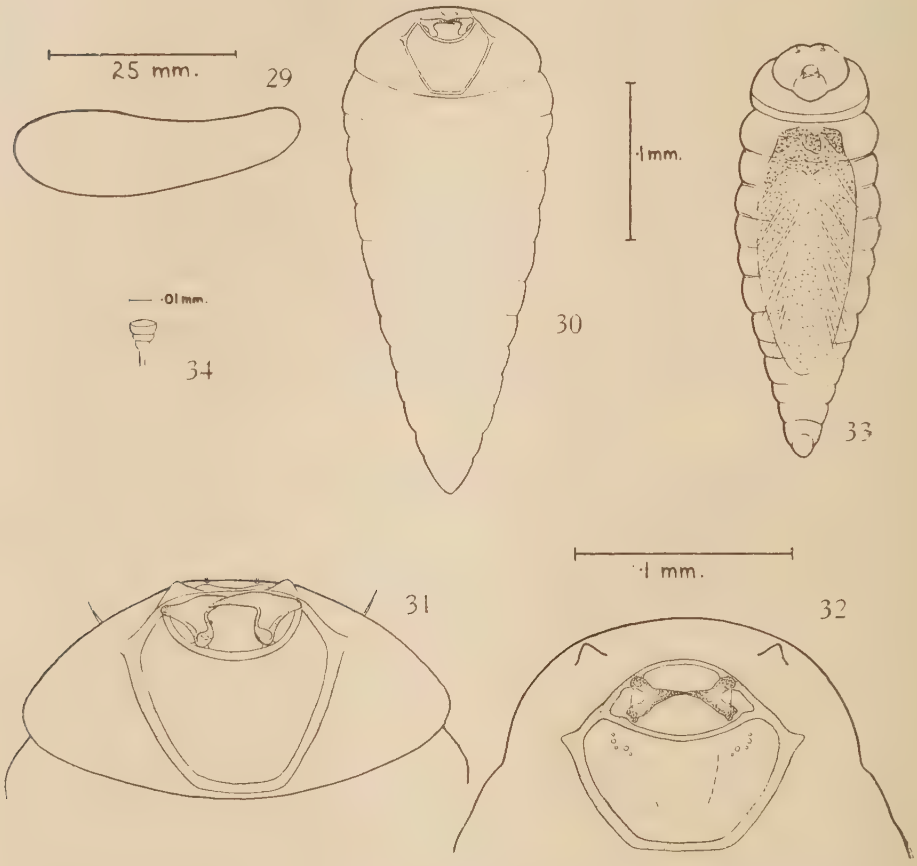


Fig. 28.—Experimental vial used for breeding *Callitula*, *Loxotropa* and *Spalangia*.

Females showed great interest in frit puparia immediately the latter were introduced into the vial and examined them in the usual way with the antennae, tapping over the whole surface of each puparium, but especially the ends. Following this examination, the ovipositor was unsheathed and thrust into the puparial shell. After puncturing the puparium and pupa, a process which occupied about half a minute, the female withdrew the ovipositor and often fed on the liquid which exuded from the pupa through the puncture. Several punctures may be made in this way before oviposition occurs and the female may move away from the puparium several times. Eggs were found only in those puparia which contained a pupa and not in those in which there was still a larva. The puncturing of the pupa paralyses it, since no further development of it occurs.

The egg is about 0·38 mm. long and 0·14 mm. wide at the widest part. It is wider at one end and is curved (fig. 29). It is translucent, waxy white, is without sculpturing, and is laid externally on the host pupa beneath the puparial shell. It is deposited anywhere on the surface, but is usually located in one of the grooves of the pupal cuticle.

The incubation period is about 2 days at 75°F. The first-instar larva (fig. 30) is cone-shaped, and is 0·30 mm. long and 0·12 mm. wide. The head capsule, shown in fig. 31, is about 0·12 mm. in width. The larva is ectoparasitic on the host pupa and after about 2–3 days ecdysis occurs, the second-stage larva then being 0·60 mm. long and 0·16 mm. wide. The head capsule is shown in fig. 32. In a further 2–3 days, the larva moults again and enters the third stage, in which it grows to a size of about 2·5 mm. long and 1 mm. wide, and devours the entire host. In this stage, it is at first elongate, but eventually it becomes a typical stout Chalcid larva (fig. 33), with the head capsule almost sunk into the body. An abdominal spiracle is shown in fig. 34. The total larval period lasts about 9–10 days at 75°F. During the last 2–3 days of this period, the full-grown larva remains motionless in the now empty host and becomes a prepupa. The pupa (fig. 35) is creamy-white at first but darkens gradually. After about 8 days, the adult emerges through a comparatively large circular hole bitten through the puparial shell at one end, giving the latter a characteristic appearance. Emergence of this species, unlike *Hexacola* and others, may occur at either end.



Figs. 29–34.—*Callitula bicolor* Spin. : (29) egg ; (30) first-stage larva ; (31) head capsule of first-stage larva ; (32) head capsule of second-stage larva ; (33) third-stage larva ; (34) abdominal spiracle of third-stage larva.

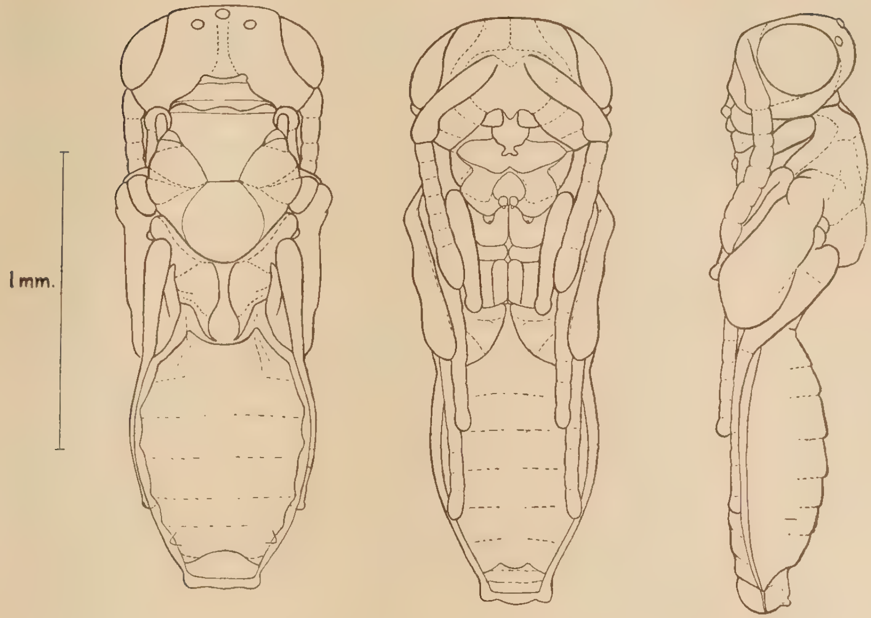


Fig. 35.—*Callitula bicolor* Spin. Pupa (dorsal, ventral and lateral).

Puparia parasitised by a single female under observation were set aside at 75°F. to ascertain the developmental period ; these gave the following results.

TABLE VI.

Days after oviposition on which emergence occurred	16	17	18	19	20	21	22	23	24	25
Males		1	3	1	4	—	4	—	1	1
Females	1	—	2	4	1	—	2	—	1	—
Totals	1	1	5	5	5	—	6	—	2	—

This gives an average of almost exactly 20·0 days, there being no significant difference between males (20·5 days) and females (19·6 days). It also shows that there were 15 males and 11 females in the 26 specimens bred. Though these numbers are small, they indicate that the sexes occur in approximately equal numbers.

This species is a primary parasite of frit puparia, and is not, as was suggested by Imms (1932), a secondary parasite. The females will, however, under exceptional circumstances, parasitise puparia containing full-grown larvae of the same and other species, but this would only occur when parasitism of the frit-fly is exceedingly high.

Females lay readily in captivity. Over 50 eggs were obtained from each of two females laying on frit puparia. Superparasitism occurred frequently in the laboratory, though only a single parasite can develop in one host puparium.

One female taken in the field on 30th June and kept at 75°F. lived until 2nd August. During this period of 33 days, it was presented with 32 puparia of frit, of which 17 were parasitised by it. A great deal of superparasitism occurred, and in one case 10 eggs were laid in a single puparium. In the laboratory, individuals kept separately at 75°F. live, in the case of males, for 11 and 26 days and females, 21, 32, 20, 33 and 62 days.

Later it was found possible to breed *Callitula* on *Drosophila* puparia. The technique was similar to that used for *Spalangia*. The parasites were reared at 70°F., 75°F. and 83°F. The biological data obtained are summarised below (Table VII).

TABLE VII.

Temperature		Length of life of females in days	Preoviposition period in days	Postoviposition period in days	Total eggs from those females that laid	Sex ratio of progeny from mated females		Developmental period (days)	
						♂	♀	♂	♀
83°F.	Maximum...	54	22	27	115			16	23
	Minimum ...	13	2	—	41			11	14
	Average ...	39·0	10·1	10·1	76·3	48·1	51·9	13·46	15·34
75°F.	Maximum...	89	42*	16	134			27	27
	Minimum ...	10	20	6	42			17	20
	Average ...	37·7	31·0	11·0	88·0	46·6	53·4	20·86	22·72
70°F.	Maximum...	63	35†	8	81			31	33
	Minimum ...	10	6	2	7			23	25
	Average ...	30·1			39·0	26·5	73·5	25·52	27·67

*Of 12 females, only two laid any eggs. Figures for pre- and postoviposition are for these two only.

†Of ten individuals only three laid any eggs.

From this table it is evident that, in contrast with individuals reared in the summer from frit, those that were reared from *Drosophila* had a long preoviposition period at all three temperatures and most of the females did not oviposit at all at the lower temperatures. It appears that the ovaries do not reach full maturity on emergence and that eggs will only mature at a high temperature. This may be due to the nutritional value of *Drosophila* puparia as hosts. When *Callitula* is reared on *Oscinella* pupae the eggs may reach maturity sooner. However this may be, this temperature effect may be partly responsible for the scarcity of this parasite in the field. Individuals which were placed on emergence in cold storage at 40°F. were found to survive well (some up to 6 months) and it is probable that the very extended preoviposition period and the ability of the adult to withstand long periods of cold may be connected with the method of overwintering. Adults emerging in the fall may overwinter before any oviposition occurs.

The length of the period of development, the length of life and the number of eggs laid suggest that *C. bicolor* could be an efficient parasite of frit-fly. Nevertheless, in America as in England, it is a relatively unimportant parasite of frit, although it breeds readily enough in the laboratory on this host. This suggests that frit is only an accidental host, and that other species are preferred hosts in the field ; no other hosts, however, have been recorded.

This species was taken in the field on 30th June 1942 and was reared from collections of frit puparia taken between 3rd July and 24th August. The stage in which it passes the winter is unknown, though the evidence given above suggests that it may do so as an adult. Adults are on the wing in the latter part of June, parasitising the frit puparia of the first summer generation, and from then are present at least until mid-August. It would seem that the spring generation of adults from overwintering material gives rise to a summer generation of adults at the end of July. In 1942, 13th July was the first date on which *Callitula* emerged in the laboratory from field material collected on 3rd July. On 23rd July, a male emerged from a collection taken on 7th July, and on 17th July, two females from a collection taken on 14th July. Had the material been left in the field, emergence would undoubtedly have been somewhat later. The last date of emergence was 9th September, when a male emerged from a collection of field material taken on 24th August. It is probable that a second generation occurred in late August and September, but the spread of dates of emergence may be due to the length of life of the ovipositing females in June and July.

(f) *Spalangia drosophilae* Ashm.

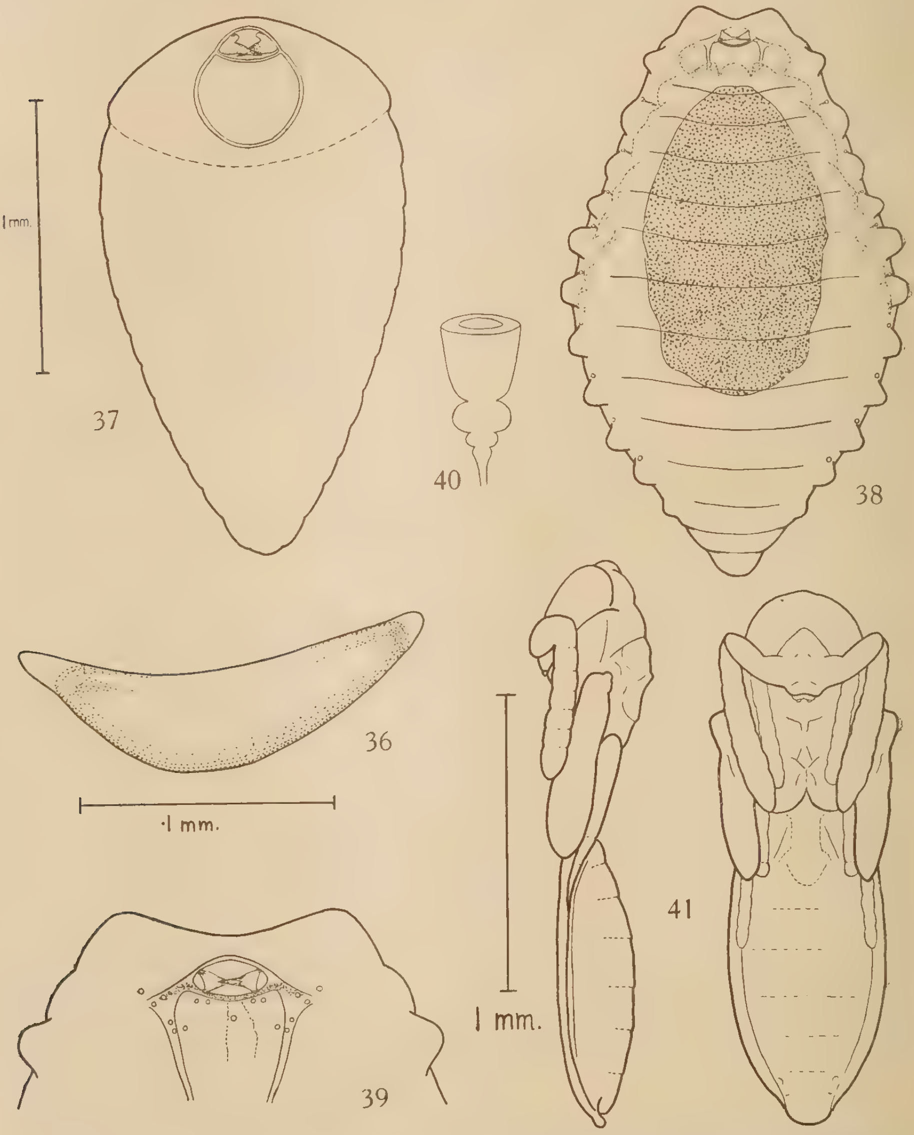
This species has not before been recorded from *O. frit*, although it was a common parasite of frit puparia in 1942. In the Parasite Catalogue, *S. drosophilae* is recorded from *Alysia ridibunda* Say (Braconid), *Psilodora rufocincta* Kieffer (Cynipoid) and *Lyperosia irritans* (L.) (Muscidae), all three by Lindquist (1936) from the U.S.A. It is a primary parasite on *Lyperosia*, but is also a hyperparasite, since the other two recorded hosts are themselves parasites of *Lyperosia*. It has also been recorded in a single instance from Trinidad parasitising a puparium of the Tachinid, *Theresia claripalpis* (Wulp), a parasite of *Diatraea saccharalis* (F.). A species of *Spalangia* (? *nigra* Latreille) was reared by Riggert in Germany in 1931 from two frit puparia taken from oats on 10th and 20th June. This is the only record of a species of *Spalangia* from frit. These two puparia were left at a laboratory temperature of 18°–20°C., but the adults did not emerge. On 1st October, one was removed, apparently healthy (Riggert does not mention in what stage it was). The second emerged on 7th January 1932. Riggert suggested that these would not have emerged under normal conditions until the following spring, which agrees very well with the behaviour of *S. drosophilae* as described below.

The species of *Spalangia* Latreille belong to a peculiar group of Pteromalids, separated by Ashmead as the subfamily Spalanginae, and by some authors as a separate family, SPALANGIIDAE. Although similar in general characteristics to the PTEROMALIDAE, Spalangiids possess a few well defined distinguishing characters. The antennae, of 8–12 joints, are inserted just above the mandibles, the head is oblong, the thorax long and depressed and the abdomen distinctly petiolate. A key to the species is given by Ashmead (1894).

On emergence, males and females of *S. drosophilae* mate readily. The male becomes excited in the presence of the female and walks towards her with wings alternately vibrating and motionless, approximately in alternate seconds. The vibration takes place with the wings half extended from the body and gives the appearance of a half-flying motion (as seen in the mating behaviour of many male Ichneumonids, such as *Cryptus sexannulatus* Grav. and *Ephialtes caudatus* (Ratz.), parasites of the codling moth). The male mounts on the female's back and strokes the latter's antennae with its own, meanwhile maintaining the periodic vibrating movement of the wings. After about half a minute of this, the male slips back and turns the tip of its abdomen under that of the female, and copulation rapidly occurs. Oviposition takes place, with or without copulation, almost immediately on emergence if suitable hosts are present.

Arrhenotokous parthenogenesis occurs with virgin females. When frit puparia are placed with females the latter show an immediate interest in them, minutely examining them, particularly the spiracular projections at the end, with their antennae. This examination, which takes several minutes, is followed by stinging, resulting in paralysis of the pupa, and by feeding at the puncture. The stinging may be repeated several times. Eventually oviposition external to the pupa occurs in the same manner as in *Callitula bicolor*. The whole procedure occupies 10 to 30 minutes.

The egg is crescent-shaped, more pointed at one end than the other (fig. 36), waxy white and about 0·17 mm. long and 0·04 mm. in maximum width. There is



Figs. 36–41.—*Spalangia drosophilae* Ashm. : (36) egg ; (37) first-stage larva ; (38) third-stage larva ; (39) head capsule of third-stage larva ; (40) abdominal spiracle of third-stage larva ; (41) lateral and ventral view of pupa.

no apparent sculpturing, the surface of the chorion being smooth. Eggs hatch in about 3 days at 75°F. The first-stage larva is conical in shape (fig. 37), has 13 segments, is 0·2 mm. long and is widest at the head capsule which measures 0·12 mm. in width. The mid-gut is filled with beige-coloured granules. The cephalic skeleton is well developed, with mandibles, epistoma, pleurostoma, hypostoma, and tentorium distinct, but only the mandibles are heavily sclerotised. Owing to the small size of the larva, facial sensoria could not be distinguished. No tracheal system could be detected. The first-stage larva feeds externally on the paralysed pupa, and becomes almost sac-like in form. Ecdysis occurs in about 24 hours. The second-stage larva is very similar to the first stage except in size, being about 0·35 mm. long and about 0·2 mm. wide. It too becomes sac-like in 2–3 days, when it moults to the third stage. Still no tracheal system is apparent.

The third-stage larva grows to a size of about 2·5 mm. in length and about 1·0 mm. in width when extended (fig. 38). It is very stout, and when seen within the puparial shell of the host appears almost globular. It is waxy white, with a conspicuous purplish faecal mass with beige globules within the body. The most outstanding character of the fully grown larva is the presence of 11 pairs of ventro-lateral lappets of the body wall, situated just ventral to the lateral line on the first 11 segments of the body. These vary slightly in shape and size as shown in the figure, and are largest about the middle of the body, where they project for about 0·1 mm. from the general body surface and are about the same measurement in length. They are turgid and conspicuous, giving the larva an appearance which distinguishes it immediately from the other puparial parasites of *O. frit*. Their function is unknown. The cephalic skeleton has a strongly sclerotised hypostoma, the remaining structures being little sclerotised, especially the epistoma which is therefore difficult to distinguish. The position of the facial sensoria is shown in fig. 39. There are 9 pairs of spiracles, on the anterior margins of segments 2–10, just in front of the anterior border of the lappets. The structure of a spiracle is shown in fig. 40. There are longitudinal tracheal trunks and a well developed tracheal system. The lateral tracheal branches leading to the spiracles seem to be blocked in the specimens examined. A detailed account of the morphology of a larva of this genus has been given by Richardson (1913), but this has been contradicted on a number of points by Parker (1924) whose observations the present work has to a certain extent confirmed.

The third-stage larva devours nearly all the remaining tissues of the host pupa, leaving the skin and undevoured part as a flattened pad lying against the puparial wall. The amount of host material that remains depends on the age of the host pupa when parasitism occurred ; a pupa in an advanced stage of development contains a greater amount of indigestible material than a younger one. The third instar, to the cessation of feeding, lasts about 4–5 days, making a total time from egg-laying to the attainment of full growth by the larva of about 11–12 days at 75°F. When fully grown, the larva becomes a prepupa, which is similar to the fully grown larva except that there is a slight alteration of body form owing to constriction of the first 3 segments. This stage lasts somewhat longer than a day. Pupation occurs between the 13th and 16th day after oviposition. The pupa is at first creamy white, but it darkens gradually to a deep blueish black in a few days. It is very variable in size, depending on the size of the host puparium and the age of the pupa when attacked. The length varies from about 1·5 mm. to 2·8 mm. and the width is about 0·7 mm. (fig. 41). The pupal stage lasts a further 6–8 days. The adult emerges through a small irregularly circular hole bitten through the puparial wall, usually at the anterior end of the puparium ; of 200 exit holes examined, 184 were anterior and 16 posterior.

In the laboratory, *Spalangia* was bred in vials on *Oscinella* puparia in the manner described for *Callitula*. Single mated females were supplied with five unparasitised frit puparia each day. From these experiments, the total developmental period of *Spalangia drosophilae* from oviposition to emergence was found to be as shown in Table VIII.

TABLE VIII.

Days after oviposition on which emergence occurred...	19	20	21	22	23	24	25	26	27	35	Total
Males	1	2	4	5	—	2	—	—	—	—	14
Females		1	2	18	28	5	1	2	1	1	59
	1	3	6	23	28	7	1	2	1	1	73

This gives an average period of 22·7 days ; the period for males averages 21·5 days, and that for females 23·0 days. Lindquist (1936) states that at an average temperature of 83·1°F., development takes 17–35 days, with an average of 22·8 days, males emerging slightly before the females.

The sex of the parasites bred (14 males and 59 females) indicates a sex-ratio of 80·8 females to 19·2 males. Of the parasites that emerged from field-collected material, 53 were males and 149 females, giving a sex-ratio of 73·8 females to 26·2 males. Arrhenotokous parthenogenesis occurs, and presumably this sex-ratio is self-regulatory, since scarcity of males and consequent parthenogenesis would produce more males in the next generation to restore the sex-ratio. However, from the point of view of biological control, this sex-ratio of approximately 3 : 1 is advantageous since a given number of parasitised hosts will produce in the following generation, not half, but three-quarters, their number of female parasites.

In the laboratory, at 75°F., the length of life of the adult *S. drosophilae* reared on *Oscinella* puparia varied considerably. Some died a few days after emergence, and others lived up to 35 days. Those under observation in vials with damp cotton and raisins lived as shown in Table IX.

TABLE IX.

Length of life in days	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Males	—	—	—	—	—	1	—	1	—	—	—	1	1	—	1	—	—	—	—	—
Females	1	—	1	1	2	1	1	5	1	4	—	3	1	2	5	2	1	2	1	—
	1	—	1	1	2	2	1	6	1	4	—	4	2	2	6	2	1	2	1	—

Length of life in days ...	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Total
Males ...	—	1	1	—	—	—	—	—	—	—	1	—	—	—	1	9
Females ...	—	—	—	—	—	—	1	—	—	—	1	—	—	1	—	37
	—	1	1	—	—	—	1	—	—	—	2	—	—	1	1	46

With such variation, figures for average length of life have little meaning, but the average figure is 18·3 days for the males and 15·4 for the females. These figures agree with those given by Lindquist (1936).

In these breeding experiments, it was found that a certain number of the parasitised hosts did not produce *Spalangia* adults, but that the fully grown *Spalangia* larvae remained as such in the empty host puparia. These larvae were found to be in a state of diapause, since raising the temperature would not induce them to form pupae. In addition to 73 that became adults in the breeding experiments (conducted at 75°F. between 4th and 22nd August, 1942), there were 19 fully grown larvae in diapause, a percentage of 20·7, and in addition to 181 adults that emerged from part of the field-collected material, there were 65 larvae in diapause, a percentage of 26·4. It is in this stage that the species passes the winter. The diapause is similar to that recorded by Riggert (1935) for the German material, and has been investigated more fully in experiments described elsewhere (Simmonds, 1948).

During the 1942 season there wĕre 273 specimens of *Spalangia drosophilae* among the 1,488 parasites that were reared ; this is 18·5 per cent. From the same collection, 2,160 frit emerged and *Spalangia* therefore formed 7·5 per cent. of all the insects that emerged. This figure is deceptive, since some of the parasites of the frit that emerged came from larvae collected in the field which had never been exposed to attack by *Spalangia*, a pupal parasite. Of the pupal parasites, which numbered 422, the 273 *Spalangia* constitute 64·7 per cent. From field-collected puparia placed in vials, 1,493 frit and 266 *Spalangia* emerged ; this gives a parasitism by *Spalangia* of 15·1 per cent.

Further discussion of the effectiveness of *Spalangia* as a parasite of frit will be postponed until a comparison of all the species is made, and it is sufficient here to add that in the week of 16th–22nd July, 1942, out of a total puparial parasitism of 53·5 per cent. (including 17 per cent. due to larval parasites), *Spalangia* accounted for 26·7 per cent. In 1943, no *Spalangia* were obtained, and the species was very rare in 1944, possibly indicating that its abundance on frit in 1942 was due to unusual conditions, perhaps abundance of host puparia at one particular period, and that usually it is not so generally abundant or else confines its parasitism to hosts other than frit.

The species was first reared from a collection of frit material made in the laboratory garden at Belleville on 30th June, 1942, from which a female emerged in the laboratory on 23rd July, indicating that parasitism had occurred only a day or two prior to collection of the materials. From a collection made on 2nd July, 4 *Spalangia* emerged in the laboratory, 2 on 31st July and 1 each on 22nd and 23rd July, again indicating that parasitism had occurred in the last week of June. Subsequent collections substantiated this, and collections of Chalcids taken in sweepings showed female *Spalangia* to be present in the field on 26th and 30th June. From a collection of puparia made on 22nd July, a male emerged in the laboratory on 25th July. This and subsequent emergences suggested that the summer generation commenced to emerge in the latter half of July. Adults continued to emerge from subsequent collections until mid-September.

It is clear that, in the spring, *Spalangia* adults emerge from overwintered larvae and, at the end of June, begin parasitising puparia of the first summer generation of frit. This parasitism reaches a maximum about mid-July and the first summer generation of *Spalangia* emerges in the second half of July and the first half of August. This generation is followed by another emerging in the second half of August and in September. About 20–25 per cent. of the fully grown larvae overwinter as such and produce adults in the spring.

Spalangia drosophilae has been investigated previously as a possible agent for controlling the horn-fly, *Lyperosia*. Its biology, with that of *Spalangia muscidarum* var. *stomoxysiae* Gir., was studied by Lindquist (1936) with the object of assessing its value for the control of *Lyperosia irritans* (L.) in the U.S.A. In 1932, Handschin introduced *Spalangia sundaica* Graham and *S. orientalis* Graham from Java to Northern Australia for the control of this pest.

Although this insect has been recorded as a secondary parasite and, in the present work, was found once as a parasite of a pupa of *Hexacola* sp. and twice as a parasite of unidentified frit parasites, secondary parasitism by it is not normal and apparently occurs only when unparasitised hosts are very few. Being an efficient pupal parasite of frit for a limited period during the summer, it might be useful in England.

Exact Host Relationships.

So far, no attempt has been made to determine whether the parasites reared are specific in their host relationships or attack frit puparia in a general way. It is important to know the exact host-relationships of each species when their potentialities as agents in biological control are being considered.

Since the cephalopharyngeal skeleton of the fully grown frit larva has characters which are of specific value, it is possible to obtain this information. Empty parasitised host puparia from which known species of parasites had emerged were dissected and identified by means of the larval mouth-parts. The results are shown in Table X. The parasite, in emerging, sometimes bites through the mouth-parts, and it may then be impossible to identify the host. Such puparia are showh in the last column as " undetermined."

TABLE X.

Exact host relationships of the various parasite species. Specific determinations of puparia from which known species of parasites have emerged.

Parasite species	Number examined	Ex *O. frit*	Ex *O. carbonaria* or *O. soror*	Ex *O. minor*	Ex *Meromyza americana*	Ex *Elachiptera costata*	Undetermined
Spalangia drosophilae	200 50♂♂150♀♀	169 36♂♂ 133♀♀	6 4♂♂ 2♀♀	18 6♂♂ 12♀♀	1 1♀	—	6 4♂♂ 2♀♀
Loxotropa sp.	100 21♂♂ 79♀♀	74 11♂♂ 63♀♀	2 2♀♀	8 3♂♂ 5♀♀	—	—	16 7♂♂ 9♀♀
Hexacola sp.	200 80♂♂ 120♀♀	92 37♂♂ 55♀♀	4 4♀♀	9 5♂♂ 4♀♀	—	—	95 38♂♂ 57♀♀
Polyscelis sp.	50	44	—	—	—	—	6
Callitula bicolor	20 9♂♂ 11♀♀	14 6♂♂ 8♀♀	1 1♂	1 1♀	—	—	4 2♂♂ 2♀♀

As the table shows, 88·7 per cent. of the parasites from determined hosts were from *O. frit*, 2·9 per cent. from *O. carbonaria* and *O. soror*, 8·1 per cent. from *O. minor* and 0·2 per cent. from *Meromyza americana*. The hosts were present in the collections examined in the proportions : *O. frit* 82·6 per cent., *O. carbonaria* and *O. soror* 6·6 per cent., *O. minor* 9·4 per cent., other species 1·3 per cent. It would therefore seem that, except in the case of *Polyscelis*, no one species of host was especially preferred by any of the parasites. In the case of *Polyscelis*, only *O. frit* was attacked in 1942, though in 1944 it was also reared from *O. carbonaria*. Examination of larger numbers of puparia might show that this parasite too attacks the other host species.

Predators.

The possibility of predators attacking the various stages of frit was not investigated, but it would seem probable that the eggs, being fairly exposed on or near the stem of wheat plant, are subject to attack. In one case, mites were found swarming over wheat plants, and they might have killed a number of frit eggs. Coccinellids are reported to destroy frit larvae (Wilhelm, 1889 ; Rörig, 1893 ; Schesterikov, 1910), but were not observed to do so in the present investigation. The only predator found was a Cecidomyiid larva which was observed eating into a frit larva lying in the tissues of the wheat stem. Had predators been common, they would certainly have been noticed, and it must be assumed that they are very rare.

Control Exerted by Parasites.

During the three seasons 1942 44, an estimate was obtained of the variation throughout the summer of the populations of both the frit-fly and its parasites in the field at Belleville. Data obtained from the samples taken and a full analysis of the results will be published later, but a brief summary of the general conclusions may be given here.

Since the main object of this investigation was to obtain parasites suitable for introduction into England to control the frit-fly, it is important to evaluate as far as possible the status of each species as a controlling agent, to determine the interaction of the populations of host and parasites, and to consider whether each species is already present in England or is represented there by one with very similar habits.

It was found that, at the beginning of the summer season, the density of the frit-fly population and parasitism are both low. Larval parasitism by *Hexacola* and *Polyscelis*, the latter attacking only third-stage larvae prior to pupation, soon begins to build up and increases steadily towards the middle of the summer. Later, it declines to some extent, possibly owing to secondary parasitism by the pupal parasites which, when larval parasitism is high, undoubtedly attack and destroy a number of puparia already containing parasitised larvae. The biology of the larval parasites, however, is such that this secondary parasitism is limited.

In early July, 1942, an increase in the degree of parasitism by *Spalangia* was probably most important in controlling the numbers of frit later in the season, since a high degree of parasitism was rapidly built up at a time when parasitism by larval parasites was not particularly high. *Spalangia* is also intrinsically superior to all the other frit parasites. The other pupal parasite, *Loxotropa*, was of greater importance later in the summer. *Callitula* played a very minor rôle throughout the period.

In 1944, *Spalangia* was rare and *Loxotropa* was the more important pupal parasite. It is obvious that in a parasite complex such as this, the importance of each species as a controlling agent varies from season to season and from week to week, and that there are many possible causes of this variation, such as the state of the host plant and the suitability of the weather in the early part of the season for the rapid build-up of the population of the host or of any of the parasite species. It is difficult, therefore, to state in this case that one particular species of parasite is the most important.

Of the two larval parasites, *Hexacola* is of greater importance than *Polyscelis*, but the latter may increase if the degree of parasitism by *Hexacola* is low. Of the pupal parasites, *Callitula* was never very important ; *Loxotropa* was much more so, particularly in the later part of the season and when *Spalangia* was rare. In 1942, *Spalangia* was very important for a short while during mid-summer. Experience with other parasite complexes suggests that the relationship of the importance of the various species would be very localised, small differences in environment in the early part of the season causing considerable variations. Nevertheless, the situation that was found to exist throughout the 1942 season at two localities 10 miles north and south of Belleville was similar to that observed at Belleville. Thus it is the efficiency of the parasite complex as a whole rather than that of its individual members that is important in this case.

This investigation has led to the conclusion that of these parasites, *Spalangia* is likely to prove the most useful if introduced into England. *Callitula* occurs in both America and England and is unimportant in both. The larval parasites, *Hexacola* and *Polyscelis*, have very similar counterparts in the parasite complex of frit-fly in England in *Rhoptromeris* and *Halticoptera*, respectively. *Loxotropa* already occurs in England. *Spalangia*, however, has no counterpart there and might serve as a controlling factor because of its ability to increase considerably when parasitism by other parasites is low.

Summary.

An account is given of an investigation made of the life-histories of *Oscinella frit* and its parasites in Ontario, Canada, with a view to the possible introduction of suitable parasites into England. The various Chloropid species associated with *O. frit* in North America are discussed.

The life-history of the frit-fly in Ontario is similar to that in England except wheat, not oats, is attacked, and that there appears to be no regular grain-infesting generation, but the insect is never a major pest in Canada.

The life-histories of the following six species of parasites are described : *Hexacola* sp. n., *Polyscelis* sp. n., *Loxotropa* sp., *Cyrtogaster* sp., *Callitula bicolor* and *Spalangia drosophilae*. Other hosts from which these parasites have been reared include Chloropids associated with *O. frit* in wheat, namely *O. carbonaria*, *O. soror*, *O. minor* and *Meromyza americana*.

A brief account is given of the control exerted by these parasites on the population of frit-fly in Ontario and a comparison is made between the Canadian and English parasite complexes. From this it is concluded that *S. drosophilae* might exert some control of frit-fly if introduced into England.

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A NEW *ANOPLONYX* DESTRUCTIVE TO LARCH IN BRITAIN (HYMENOPTERA : TENTHREDINIDAE).

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All the leaf-feeding sawflies on *Larix* in Britain belong to the Nematine Tenthredinidae. Up till a few years ago, the most notorious recorded in this country was *Pristiphora erichsonii* (Hartig), though local attacks of *P. wesmaeli* (Tischbein) and *P. laricis* (Hartig) have also occurred. These are also the chief Tenthredinid enemies of larch on the European continent, where the genus *Anoplonyx* has apparently never occurred in sufficiently large numbers to cause economic damage. In Britain, where larch is not a native tree, the sawflies attacking its leaves are all restricted to it and so must have been introduced into the country.

The genus *Anoplonyx* belongs to the more generalised of the Nematinae and is clearly defined taxonomically (Ross, 1937, pp. 81–82) ; it has very few known species, four in North America and four (including the new one described herein) in Europe. It is entirely associated with *Larix*, and among themselves the species are closely similar and difficult to distinguish. *Anoplonyx* in the adult stage is at once distinguished from *Pristiphora*, the other larch-feeding genus in Britain, by having an inclosed basal lobe to the anal cell in the forewing.

The British species of *Anoplonyx* was first recorded by Cameron (1885, p. 223) on the strength of a single female, which he called " *Camponiscus apicalis* Zaddach ", captured at Weybridge, Surrey, by T. R. Billups. Morice (1904, pp. 246–247) calls this species " *Leptocercus duplex* Lepeletier ", following Konow's synonymy, and in his collection are five British specimens, one of them determined by Konow himself.

In recent years, especially with the extensive planting of larch, this sawfly has become increasingly evident in Britain. In 1947, a serious outbreak was noticed at Craigvinean, near Dunkeld, Perthshire, and in Warren Wood on the Atholl Estate, nearby. Here it defoliated many acres of both the Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gord.) and the European larch (*L. decidua* Mill.).

It has been known for a long time that there existed certain differences between this species and that known as *Anoplonyx duplex* in central Europe. For instance, the larva of the British species is green with four longitudinal brown stripes, and is entirely unlike the brown- and black-flecked muddy-green larva ascribed to *duplex* by Enslin (1915, p. 325) and Hsin (1935, p. 281), and whereas Enslin described a male, the British species is apparently entirely parthenogenetic. In head structure and wing venation, the latter species appeared to agree much more closely with *ovatus* (Zaddach) than *duplex*, but it differed from *ovatus* in antennal and other characters. The occurrence in this country of a parthenogenetic strain of a species reproducing sexually further south is not unusual in sawflies, and the importation of parthenogenetic forms can obviously result more easily in the establishment of a species, as a single female can start a new colony. This is shown by the fact that many of the most serious imported sawfly pests (*Caliroa cerasi* (L.), *Gilpinia hercyniae* (Hartig) and *Pristiphora erichsonii* (Hartig)) are parthenogenetic strains. The entirely different larva suggested, however, either that our species was not the one known on the continent as *Anoplonyx duplex* or that the larva ascribed to *duplex* on the continent was of some other species.

The problem has remained unsolved till now, but faced with having to include the species in my synopsis of British sawflies and with the need for intensive research into its biology, I have recently been making a closer study of the taxonomy of this genus in Europe. When I wrote for material of it from other parts of Europe for study, another interesting fact came to light ; outbreaks of *Anoplonyx* as a pest are virtually unknown in Europe apart from Britain and, as a result, material of the genus was extremely scarce in European Museums. In fact, Dr. Nägeli in Switzerland, Drs. Francke-Grossman and Thalenhorst in Germany, and Dr. Forsslund in Sweden were unfamiliar with the species of this genus as forestry insects, though in N. America, " Marlatt's Larch Sawfly " (*A. luteipes* Cresson (=*laricis* Marlatt) is a well-known forestry pest. I am indebted to Dr. Kühlhorn of the Zoologische Staatssammlung, München, for lending me material from the Enslin and Kriechbaumer collections, to Professor G. C. Varley of the Hope Department of the University Museum, Oxford, for material from the Morice collection, to Mr. Kontuniemi of Helsingfors for sending me material from Finland, to Messrs. H. S. Hanson and M. Crooke of the Forestry Commission for supplying me with information and fresh British specimens, and also to Dr. H. H. Ross and Mr. L. J. Stannard of Illinois for sending me representatives of North American species. With the help of this material, I have been able to see 19♀♀ and 2♂♂ of *A. ovatus*, 8♀♀ and 3♂♂ of *A. duplex* 8♀♀ and 10♂♂ of *A. pectoralis*, and 160♀♀ of the British species.

Slight morphological differences in the head, correlated with the parthenogenetic habit and larval colour pattern, indicate that the British species is not *A. duplex*, as it has heretofore been named following the opinion of Konow himself, and it has not been possible to identify it with any of the other known palaearctic or nearctic species. The position is thus one of peculiar interest ; we have a sawfly pest of larch in Britain which has not been recognised as existing in any other country, though Mr. Kontuniemi of Helsingfors has sent me two specimens of it from Finland where he says it is very rare. The position is somewhat similar to that of the early stages of the investigation into the outbreak of *Gilpinia hercyniae* (Hartig) in Canada ; here also was an unknown species not at first known to occur in what later proved to be its native continent, Europe, and likewise distinguished from its nearest known relatives by its parthenogenetic habit.

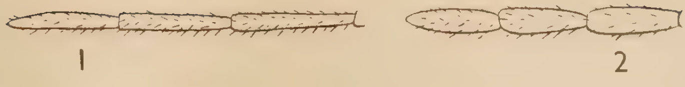
Anoplonyx destructor, sp. nov.

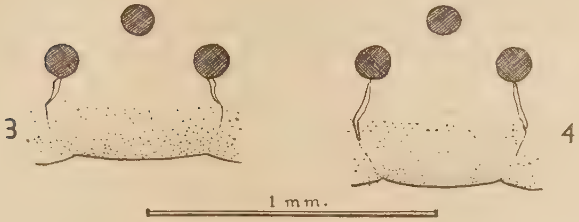
♀ Black with the following parts yellowish or brownish white : palps, more or less apex of labrum and of pronotum, tegula, more or less sides of mesonotum, trochanters, apex and more or less upper side of front and middle femora, hind femur at apex and above, tibiae and tarsi of all legs and more or less last abdominal segment with cerci ; underside of abdomen more or less piceous. Wings hyaline ; stigma with C and Sc yellowish white ; rest of venation brownish white. Length 4·5–6·5 mm.

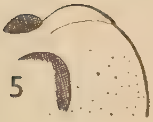
Head and thorax almost impunctate though mesoscutellum and its post-tergite may be slightly rugulose ; abdomen alutaceous. Whole insect except dorsal surface of abdomen covered with fine pubescence except for a glabrous patch in the front and also at the back of the mesosternum.

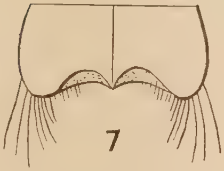
Head with clypeus slightly marginate medially in front ; frontal area with a more or less shallow medial groove confluent in front with the deeper antennal groove. Hind ocelli further apart than the distance of one from the eye margin (POL : OOL= 1·0 : 0·9) and than the distance of one from the hind margin of the head (1·0 : 0·7) (figs. 3 & 5). Antenna as long as $C + \frac{1}{2}$ stigma : fourth segment longer than third, third = fifth, sixth to ninth decreasing in length, eighth 6–7 times longer than greatest breadth (fig. 1). Wings with veins 2r and 2rm missing from forewing, or if 2rm is present then cell 2Rs is broader than long ; vein 2m-cu in forewing usually closer to 3rm than length of 3rm.

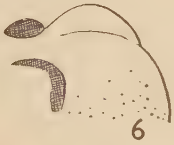
Sawsheath broad and in dorsal aspect, broader apically than the apex of the hind tibia, and emarginate each side of the middle so that it is trifid behind (fig. 7).











Figs. 1–2.—Apical segments 7, 8 and 9 of antenna (lateral view). (1) *Anoplonx destructor* ; (2) *A. ovatus.*

Figs. 3–4.—Post-ocellar region of head (from above). (3) *A. destructor* ; (4) *A. duplex.*

Figs. 5–6.—Post-ocellar region of head (lateral view). (5) *A. destructor* ; (6) *A. duplex.*

Fig. 7.—Sawsheath of *A. destructor* from above (scale ×2).

Saw typical for the genus and scarcely distinguishable from that of *A. pectoralis* (Lepeletier). ♂ unknown.

Holotype : England, Herts, Tring, 1♀, 21.v.1942 (*R. B. Benson*). In the British Museum (Natural History).

Paratypes : 156 ♀♀ from Devon, Gloucester, Sussex, Surrey, Berks, Bucks, Herts, Cumberland and Northumberland in England ; Montgomery in Wales ; Perthshire and Inverness in Scotland. May and June.

Key to European Species of Anoplonyx.

1. Antenna longer (in ♂ much longer than C+ stigma of forewing ; in ♀ at least as long as C) and thinner (eighth segment 6–7 times longer than its greatest breadth) (fig. 1). Mesosternum as well as mesopleura mainly covered with fine pubescence. Sawsheath slightly emarginate at apex in dorsal view and as wide or wider than apical width of hind tibia (fig. 7). 5·5–6·5 mm..........2

Antenna shorter (in ♂ about as long as C+ stigma of forewing ; in ♀ shorter than C) and stouter (eighth segment only about four times longer than its greatest breadth) (fig. 2). Pubescence denser on mesopleura than on mesosternum which is almost glabrous. Sawsheath subtruncate in dorsal aspect and narrower at apex than apical width of hind tibia. 4·5–5 mm.

(Frontal area of head only slightly concave with a frontal groove stretching forward from the front ocellus and more or less joining the antennal groove. Post-occipital area very short and convex: the hind ocelli are further apart than each is from the hind margin of the head in the proportion of about 3 : 2 (*cf.* figs. 3 & 5). Subalpine Regions of Central Europe: France, Switzerland, Germany, Austria, Italy. Larva, see Thielmann 1938.)...*ovatus* (Zaddach)

2 (1). Mesonotum of ♀ mainly black with at most yellowish flecks on sides of front lobe and scutellum; abdomen mainly black above though it may be more or less brownish at apex beneath. ♂ abdomen entirely black..................3

Mesonotum of ♀ yellowish brown with 3 black flecks—one occupying the central part of the front lobes and one on the inner part of each of the side lobes; mesopleura yellowish brown above but black below and on the mesosternum; abdomen yellowish brown, more or less infuscate at the base above. ♂ with underside and more or less apex of abdomen yellowish brown.
(Frontal area of the head scarcely raised and usually with a clearly defined medial groove stretching forward from the front ocellus; this groove often extends forward to join the antennal groove. Hind ocelli about as far apart as either of them is from the hind margin of the head (*cf.* figs. 4 & 6). Forewing with cross-vein 2rm present (with 4 cubital cells). Sawsheath truncate in dorsal aspect or slightly emarginate at apex and distinctly wider than the apical width of the hind tibia. 6–7 mm. Subalpine Regions of Central Europe: France, Germany and Austria. Larva, see Thielmann 1938.)...*pectoralis* (Lepeletier)

3 (2). Forewing with vein 2rm present (with 4 cubital cells). Frontal area of head more or less in the form of a basin with its medial groove separated in front from the antennal groove. Distance between the hind ocelli about the same as the distance of an ocellus from the hind margin of the head (figs. 4 & 6). ♂ and ♀.
(Central Europe and Siberia. Larva, see Enslin 1915, p. 325 after Carpentier, and Hsin 1935, p. 281; much as in *A. pectoralis*.)..............
duplex (Lepeletier)

Forewing with vein 2rm usually missing (usually with only 3 cubital cells). Frontal area more or less concave with its medial groove confluent in front with the antennal groove. Distance between hind ocelli about one-third greater than the distance of one of the ocelli from the hind margin of the head (figs. 3 & 5). Parthenogenetic species; ♂ unknown.
(Throughout Britain and in Finland. Larva green with four longitudinal stripes on body.)...*destructor*, sp. nov.

Synonymy of *A. braunsii* (Konow 1884).

Several other species of European *Anoplonyx* have from time to time been described and later sunk into the synonymy. From these descriptions, it is quite clear that *A. braunsii* (Konow) with its short antennae and characteristic venation is a synonym of *A. ovatus* (Zaddach) (**syn. nov.**) rather than of *A. duplex* (Lepeletier) with which it was synonymised by Enslin (1915, p. 325).

Comparison of North American with European Species.

Before the British species had been identified in the sample from Finland, representatives of three of the four species described from North America were borrowed to see whether by any chance the British species had been introduced from there. *A. luteipes* (Cresson) of the eastern States is close to *ovatus* and would run to this species in the key to European species given above, having very short antennae, a sub-glabrous mesosternum, a short post-ocellar area and an ill-defined frontal basin on the head, but the sawsheath is of quite different form, broadening behind in dorsal view so that it is broader at the apex than the apical width of the hind tibia, and apically it is trifid, emarginate each side of the middle. *A. occidens* Ross likewise has very short antennae, but has the pubescence of the underthorax, the venation and longer postocellar area characteristic of *duplex* and *pectoralis*. *A. canadensis* Harrington has the sub-glabrous mesosternum, short postocellar area and venation characteristic of *ovatus* but a sawsheath apically emarginate, long antennae and a head with a well-defined frontal basin.

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THE EMERGENCE AND SEX RATIO OF *CULEX FATIGANS* WIED. (DIPTERA, CULICIDAE) IN LABORATORY EXPERIMENTS.

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There is an imposing array of conflicting views on the subject of sex ratio and order of emergence of the two sexes of adult mosquitos whether laboratory-bred or occurring naturally. While there are those who believe that males show preponderance in the early batches and also collectively, there are just as many who are unable to confirm this view and have, on the other hand, observed no regularity in the order of hatching, and either noted parity of sexes in all cases or an exceedingly large number of females in the total output.

Rees (1901) found that when mosquitos are bred in captivity, the males, as a rule, emerge first and in greater numbers than the females. Stephens and Christophers (1908) record that males preponderate in artificially raised colonies. Bacot's (1916) observations in West Africa are in conformity with those of Rees (*l.c.*). About *Stegomyia* he remarks : ". . . the early males being usually a day quicker in their development than the females". Gordon (1922) observed a greater preponderance of males during the first few days of emergence than could be explained by the higher proportion of males to females. Mehta (1934) observed variations in the order of hatching of the sexes.

Regarding sex ratio, Young (1922) records a higher proportion of males among laboratory-bred mosquitos. Harold (1923), in *Anopheles maculipennis* Mg., and Mayne (1925), in some *Culex*, have obtained three males to one female and six and seven males to one female respectively.

In marked contrast to these observations are those of workers like Nuttall and Shipley (1902), Ross (1911), van Breeman (1920), Lamborn (1922), Russell (1925), Bradley (1926), Buxton and Hopkins (1927), Boyd (1930), Mehta (*l.c.*), and Sen (1935), who either assert that there exists a 1 : 1 ratio in the sexes or that the females predominate.

During the course of the present experiments, which were conducted at room temperature with a view to studying egg, larval and pupal durations in *Culex fatigans* Wied. at different times of the year, a certain regularity in the order of hatching of the two sexes and the preponderance of one sex over the other in the early and late batches reared from the same brood of eggs was noticed. In view of this an attempt was made to find answers to the following vital questions:—

1. Whether the sexes emerged in any special order.
2. Whether the total emergence was in favour of one of the two sexes.
3. Whether mortality in the early stages affected sex ratio.
4. Whether sex ratio was affected by differences in the type of food during larval life.
5. Whether temperature exercised any influence on the proportion of sexes.

Material and Methods.

Eggs obtained from gravid females of *Culex fatigans* caught in nature were reared in china bowls of standard size (diameter about 12 cm. and depth about 6 cm.) of about 270 cc. capacity. The food supplied was egg powder, and in some experiments crushed yeast tablets were also given to study the effect of different types of food on sex ratio. Tap water was used with just sufficient egg powder to give a creamish colour to the solution and it was changed daily. The pupae that formed were transferred to small cotton-plugged specimen tubes, 12 being the highest number of pupae placed in a single tube of diameter 2 cm. The sexes of the emerging adults were carefully examined and recorded. The larval mortality was recorded by counting the larvae every day in each experiment. In all, 70 such experiments were performed successfully between January and December 1950.

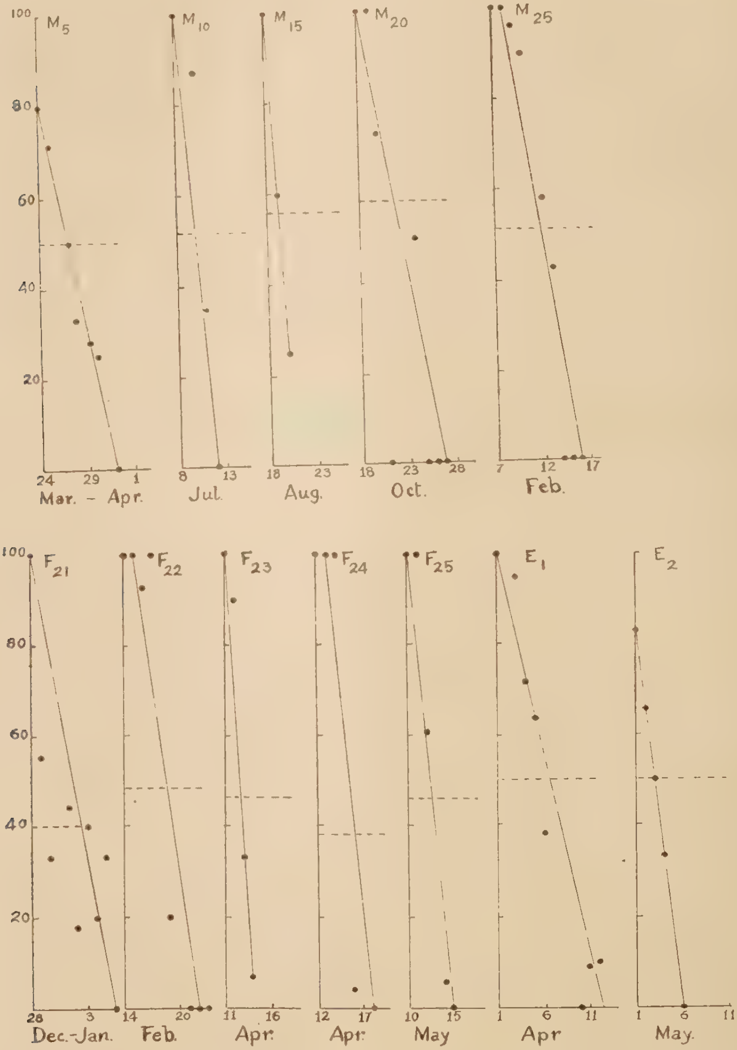


Fig. 1.—The early emergence of males shown as successive percentages ; abscissa, dates on which the batches hatched ; ordinate, percentage males of the total adults emerging in each batch. Dotted line is the mean percentage of males over the whole emergence period.

Order of Emergence of the two Sexes.

In order to confirm the impression gained during the course of these experiments that males emerge earlier than females, the data have been analysed in three different ways.

(*a*) There is considerable variation in the duration of the early stages in different individuals emerging from the same batch of eggs obtained from a single female. As a result the emerging adults fall into a number of batches hatching out successively. Graphs (scatter diagrams) showing the percentage males in the total number of adults emerging in each batch have been prepared side by side, the mean percentage of males over the whole emergence period for each experiment being indicated for comparison. On the character of sex ratio, to be discussed later, the experiments are grouped into two classes, *viz.* (i) those showing male preponderance, (ii) those showing female preponderance. To avoid any special bias in the selection of data for these graphs (fig. 1), and for the sake of brevity, five from each set of experiments bearing multiples of five as their serial number in Table I (M_5–M_{25}) and F_{21}–F_{25} in Table II have been used for the purpose. Figures of two more such experiments (not tabulated) that show a parity of sexes (E1, E2) are also graphically represented.

From a study of the graphs in fig. 1, it would appear that in all experiments there is a steady downward trend in the percentage of males emerging until a complete absence of males is recorded at the latter end of the majority of the experiments. Thus, it is clear that the males emerge earlier than females. Further, that the higher percentage of males in the early batches of an experiment bears no relation to the sex ratio in the total output is evident from the fact that preponderance of males in early emergences is as prevalent in the experiments with female preponderance as it is in those showing a sex ratio in favour of the males.

(*b*) A second method of demonstrating that the males emerge significantly earlier than the females was to divide the period of each experiment into two equal parts. From the number of males emerging in the first half (Tables I and II, col. 7) and the total males (col. 2) the percentage of males emerging in the first half was determined and the figures for each experiment tabulated. The test of significance λ^2 has been applied to each case and the value set out in column 9, with the corresponding value of P in column 10. In the overwhelming majority of these experiments the value of P is $< \cdot 01$, indicating that in the first half of the experiment the male percentage is significantly higher than in the second. The sign of plus (+ + + and + +) has been used to designate the level of significance. The highest value of p for a moderate level of significance is set at 0·05. In all the experiments, 2,979 out of a total number of males of 3,675, *i.e.*, 81·1 per cent., hatched during the first half.

(*c*) A third method of demonstrating the earlier emergence of males was to determine the lengths of the stages in the development of both males and females and to show that the differences were statistically significant. Buxton and Hopkins (1927) have shown that the length of larval life, especially of the fourth stage, is materially longer for females than for males. The results of the present experiments are in conformity with this ; whilst no difference in the egg duration in the two sexes has been detected nor any appreciable variance in the pupal life of males and females, the larval life of males is distinctly shorter than that of the females in the same brood. This fact will be clear from Table III in which the duration of the larval stage in the two sexes in each month of the year is set out. The range in the number of days, the mean larval duration for the month and the standard deviation of the mean for each sex estimated by dividing the sum of the squares of the deviation from the mean in each emergence during the month by the total number of degrees of freedom (number of observations, *i.e.*, the number of mosquitos in this case) have been tabulated. Notwithstanding the fact that there exists a

TABLE 1.

Data regarding experiments showing male preponderance in the total.

S. No.	M.T. °F. 1	♂♂ 2	♀♀ 3	S.R. 4	X² 5	P 6	♂♂ in first half 7	% ♂♂ in the first half of the total ♂♂ emerging 8	X² 9	P 10	Remarks 11
1.	65·61	28	15	100 : 53	2·333	0·20	21	75·0	3·5000	0·05	+ +
2.	68·04	40	37	100 : 92	0·0584	0·80	19	47·5	0·0500	0·8	− − −
3.	75·95	49	38	100 : 77	0·6954	0·30	40	81·5	9·8061	<0·01	+ + +
4.	77·29	76	68	100 : 89	0·2089	0·70	61	80·2	13·9210	<0·01	+ + +
5.	77·28	71	66	100 : 93	0·0668	0·70	56	78·8	11·8380	<0·01	+ + +
6.	81·31	29	19	100 : 66	1·0417	0·30	23	79·0	4·9827	0·02	+ + +
7.	83·62	62	47	100 : 76	1·0321	0·30	41	66·1	3·2220	0·05	+ +
8.	84·95	69	64	100 : 92	0·9390	0·70	52	76·0	8·8760	<0·01	+ + +
9.	84·57	63	59	100 : 93	0·0656	0·80	54	85·1	16·0710	<0·01	+ + +
10.	84·92	92	81	100 : 88	0·3468	0·70	86	93·4	34·782	<0·01	+ + +
11.	88·37	61	30	100 : 50	5·2802	0·05	52	85·2	15·1520	<0·01	+ + +
12.	84·75	41	21	100 : 53	3·2258	<0·10>0·05	14	34·1	—	—	—
13.	84·85	54	46	100 : 85	0·3200	0·70	47	87·0	14·8140	<0·01	+ + +
14.	86·12	35	28	100 : 80	0·3889	0·70	33	94·2	13·7280	<0·01	+ + +
15.	86·12	42	33	100 : 77	0·5400	0·50	40	95·2	17·1900	<0·01	+ + +
16.	85·86	48	41	100 : 85	0·2753	0·70	47	97·9	22·0420	<0·01	+ + +
17.	86·57	73	54	100 : 74	1·4213	0·30	41	56·2	0·5550	0·50	− − −
18.	86·17	40	32	100 : 80	0·4444	0·50	40	100·0	20·0000	<0·01	+ + +
19.	85·92	75	56	100 : 75	1·3779	0·30	74	98·7	36·0600	<0·01	+ + +
20.	81·25	58	40	100 : 69	1·6530	0·20	55	94·8	23·3100	<0·01	+ + +
21.	74·86	37	28	100 : 75	0·6231	0·50	34	91·9	22·7170	<0·01	+ + +

TABLE I.—(*cont.*)

S.No.	M.T. °F. 1	♂♂ 2	♀♀ 3	S.R. 4	X^2 5	P 6	♂♂ in first half 7	% ♂♂ in the first half of the total ♂♂ emerging 8	X^2 9	P 10	Remarks 11
22.	74·26	44	34	100 : 77	1·7778	0·20	39	88·6	13·1360	<0·01	+ + +
23.	77·53	41	32	100 : 80	0·5548	0·50	39	95·1	16·6950	<0·01	+ + +
24.	71·95	50	38	100 : 76	0·8182	0·50	46	92·0	17·6400	<0·01	+ + +
25.	69·24	108	99	100 : 91	0·2174	0·70	81	75·0	13·5000	<0·01	+ + +
26.	75·18	69	66	100 : 95	0·3333	0·70	68	91·3	32·5300	<0·01	+ + +
27.	75·00	33	23	100 : 69	0·8929	0·50	23	69·7	12·5600	<0·01	+ + +
28.	78·00	60	55	100 : 91	0·1028	0·70	41	68·3	4·0330	0·05	+ +
29.	79·59	69	59	100 : 85	0·4098	0·50	61	88·4	63·8330	<0·01	+ + +
30.	80·27	63	30	100 : 47	5·8548	0·02	36	57·1	0·6430	0·5	− − −
31.	79·92	66	65	100 : 97	0·0038	0·95	11	16·7	—	—	—
32.	81·73	51	18	100 : 35	7·8913	·01	44	86·3	13·3230	<0·01	+ + +
33.	84·00	79	63	100 : 79	0·9014	0·30	61	77·2	11·7020	<0·01	+ + +
34.	81·94	73	43	100 : 59	3·8793	·05	62	84·9	5·1660	0·05	+ +
35.	83·37	75	53	100 : 70	1·8906	0·20	62	82·7	16·6660	<0·01	+ + +
36.	86·50	63	60	100 : 95	0·0037	0·95	40	63·5	4·5870	0·05	+ +
37.	85·27	139	93	100 : 66	4·5603	0·05	124	89·2	42·7370	0·05	+ +
38.	85·23	69	62	100 : 89	0·3740	0·50	66	95·7	28·7610	<0·01	+ + +
39.	87·23	76	75	100 : 98	0·0033	0·95	66	86·8	20·6320	<0·01	+ + +
40.	84·66	56	55	100 : 98	0·0045	0·95	56	100·0	28·0000	<0·01	+ + +
		2,427	1,926	100 : 79	28·8308	<0·01					

M.T.°F—Mean temperature during the period of the experiment ; S.R. sex ratio ; − − −, not significant ; + +, + + +, significant at moderate and high levels respectively.

TABLE 11.

Data regarding experiments showing female preponderance in the total.

S. No.	M.T. °F. 1	♂♂ 2	♀♀ 3	Sex ratio 4	X^2 5	P 6	♂♂ in the first half 7	% ♂♂ in the first half of the total ♂♂ emerging 8	X^2 9	P 10	Remarks 11
1.	71·88	30	39	100 : 130	0·1785	0·70	17	56·6	0·2666	0·50	− − −
2.	74·00	58	64	100 : 110	0·1475	0·70	40	69·0	4·1725	0·05	+ +
3.	75·77	39	60	100 : 154	2·2271	0·10	28	72·0	3·7051	0·05	+ +
4.	77·42	55	60	100 : 109	0·1087	0·70	43	78·1	8·7363	$<0·01$	+ + +
5.	79·17	57	67	100 : 118	0·4032	0·50	55	96·5	24·6403	$<0·01$	+ + +
6.	80·18	41	68	100 : 166	3·3440	0·05	31	75·6	5·3787	0·02	+ + +
7.	80·52	51	61	100 : 120	0·4901	0·50	42	82·3	10·6765	$<0·01$	+ + +
8.	84·70	38	42	100 : 110	0·1000	0·70	36	94·5	15·2105	$<0·01$	+ + +
9.	86·75	3	8	100 : 266	1·1363	0·30	2	66·6	11·6666	0·70	− − −
10.	84·75	14	30	100 : 214	2·9090	0·10	8	57·1	0·1428	0·70	− − −
11.	83·55	33	67	100 : 203	5·780	0·02	26	78·7	5·4697	0·02	+ + +
12.	83·33	22	47	100 : 213	4·5290	0·05	21	95·4	9·0909	$<0·01$	+ + +
13.	82·78	38	46	100 : 121	0·3809	0·70	20	52·6	0·0526	0·80	− − −
14.	83·82	22	44	100 : 200	3·6666	0·05	13	59·0	0·3636	0·50	− − −
15.	83·86	49	54	100 : 110	0·1213	0·70	31	63·2	1·7245	0·50	− − −
16.	87·62	49	52	100 : 106	0·0445	0·80	41	83·6	11·1122	$<0·01$	+ + +
17.	82·92	18	24	100 : 133	0·4285	0·50	12	66·6	1·0000	0·30	− − −
18.	84·69	56	68	100 : 121	0·5806	0·50	52	92·8	20·5714	$<0·01$	+ + +
19.	80·31	40	48	100 : 120	0·3636	0·70	37	92·5	14·4500	$<0·01$	+ + +
20.	73·56	31	35	100 : 113	0·1212	0·70	30	96·7	13·5645	$<0·01$	+ + +
21.	68·00	37	53	100 : 143	1·4222	0·20	28	75·6	4·8919	0·02	+ + +
22.	68·48	66	72	100 : 109	1·3043	0·30	62	93·9	25·4848	$<0·01$	+ + +
23.	80·07	41	48	100 : 117	0·2753	0·70	28	68·2	2·7439	0·10	− − −
24.	79·95	38	62	100 : 163	2·8800	0·10	38	100·0	19·0000	$<0·01$	+ + +
25.	83·86	71	84	100 : 118	0·5451	0·50	67	94·3	27·9507	$<0·01$	+ + +
26.	85·64	45	48	100 : 106	0·0484	0·80	39	86·6	12·1000	$<0·01$	+ + +
27.	83·00	53	54	100 : 101	0·0046	0·95	40	75·4	6·9717	$<0·01$	+ + +
28.	82·06	44	45	100 : 102	0·0056	0·95	39	88·6	13·1364	$<0·01$	+ + +
29.	76·13	33	35	100 : 106	0·0294	0·90	25	75·7	4·3788	0·02	+ + +
30.	82·35	76	77	100 : 101	0·0032	0·95	72	94·7	30·4222	$<0·01$	+ + +
		1,248	1,562	100 : 125	17·5430	$<0·01$					

very obvious difference in the means for the two sexes (*cf.* cols. 3 & 6 in Table III), it was felt that statistical evaluation of the data was needed owing to the wide range in the number of days (4 to 21 in ♂♂ and 4 to 26 in ♀♀) occupied by the larval life. For this purpose the standard error of the difference of two means, *viz.*, for males and females, has been calculated for each month from the formula.

$$\text{S.E.} = \sqrt{(\text{SD}_1)^2/n_1 - (\text{SD}_2)^2/n_2}$$

where SD_1 is the standard deviation for males and SD_2 for females and n_1 and n_2 are the degrees of freedom contributed by the two sexes separately. Applying the accepted principle that the difference is significant if the two means differ by more than twice the value of its standard error we find that the difference in the means for males and females for each month is highly significant. Further, the difference of the two means for each month is subjected to the t test of significance by using the formula

$$t = \frac{\bar{x} - \bar{x}^1}{s} \sqrt{\frac{(n_1+1)\,(n_2+1),}{n_1+n_2+2}}$$

in which $\bar{x} - \bar{x}^1$ is the difference of two means, s the standard error of the difference and n_1 and n_2 are the degrees of freedom contributed by males and females respectively. The value of P for each value of t is estimated with the help of Fisher's (1950) table of t, and it is noted that in no case, except in the month of June in which the number of observations is very small owing to the scarcity of gravid females in nature (hence not considered), is there any likelihood of the difference having arisen by chance.

It is, therefore, concluded that the larval life of males is significantly shorter than that of females. Since there is no appreciable difference in the pupal life of the two sexes, it is the shorter larval life of the males that causes them to emerge earlier.

Sex Ratio.

Out of a total of 70 experiments conducted in the laboratory under almost uniform conditions, 40 showed a favourable male sex ratio and the remaining 30 a female preponderance. The figures for experiments with male and female preponderance are set out in columns 2–6 of Tables I and II in which totals, sex ratios and the respective values of χ^2 and P are tabulated. Let us now consider (1) the ranges of sex ratio, (2) the sex ratio in individual experiments and its significance, (3) the level of significance of sex ratio in the two sets of experiments considered separately, and (4) together.

(1) *The ranges of sex ratio.*—Treating the experiments as 70 different "samples" representing the same "population", a consideration of the range in sex ratios shows that the whole population can be divided into three groups.

The first group comprises 23 experiments in which the ratio of males to females ranges from 100 : 35 to 100 : 80 and may be designated as one with a "low" female ratio. The second group, which constitutes the majority of the experiments, *i.e.*, 37, shows a sex ratio of from 100 : 81 to 100 : 125. These experiments with a "moderate" female ratio tend to show a parity of sexes and greatly influence the gross sex ratio of the whole population. There is a third group in which there are only six experiments, which record a range in sex ratio from 100 : 126 to 100 : 180. Of the remaining four experiments, one with a male to female ratio of 100 : 266, is omitted owing to the very small size of the brood. A fourth group, which has not been considered as such, owing to the very high sex ratio in favour of the females, comprises only three experiments with a range from 100 : 200 to 100 : 214.

(2) The preponderance of males in individual experiments is not statistically significant, with the exception of experiments 11, 30, 32, 34 and 37 in which the

TABLE III.

Showing larval duration of males and females by months.

(——————) (–Days———) (——————)

1 Month	2 Range in ♂♂	3 Mean ♂♂	4 S.D. ♂♂	5 Range in ♀♀	6 Mean ♀♀	7 S.D. ♀♀	8 S.E.	9 Sig. t. test	10 Remarks
Jan.	12–20	14·40	2·51	13–23	17·05	2·61	0·5531	+++	
Feb.	13–19	15·92	1·55	15–24	19·35	1·15	0·1491	+++	
Mar.	5–16	9·49	1·69	5–15	10·70	2·11	0·4557	+++	
Apr.	5–21	9·30	3·31	6–26	12·72	4·47	0·2865	+++	
May	5–14	8·01	2·85	5–14	9·05	2·68	0·2912	+++	
June	5–5	5·00	0·00	5–5	5·00	0·00	—	—	Data being insufficient not considered.
July	4–12	6·48	1·46	5–11	8·74	1·84	0·1578	+++	
Aug.	4–15	7·38	1·80	4–14	10·56	1·77	0·1350	+++	
Sept.	4–11	7·23	1·59	5–13	8·88	1·40	0·1100	+++	
Oct.	5–12	6·55	1·09	6–13	8·48	1·23	0·1024	+++	
Nov.	5–13	8·21	1·15	5–14	9·30	1·67	0·1392	+++	
Dec.	8–11	9·51	1·08	9–16	12·76	1·60	0·3006	+++	

S.D., Standard deviation ; S.E., Standard error of the difference of two means ; Sig. t. test, t. test of significance.

value of P (*cf.* Table I, col. 6) is 0·05 or <0·05. Out of the 30 experiments with a favourable female ratio only four (6, 11, 12 and 14) show a significant departure from 1 : 1.

(3) It is interesting to note that while only 12·5 per cent. of the one set of experiments and 13·0 per cent. of the other depart significantly from 1 : 1, the data for each set of experiments when considered *in toto* but severally from the other set give a highly significant disparity in numerical strength of the two sexes.

(4) When the total figures (3,675 males and 3,488 females) for the two sets of experiments are added together, it is noted that the above disparity disappears and we reach an almost 1 : 1 ratio (100 : 79+100 : 125 :: 100 : 100 approximately, Tables I and II). Thus, it is evident that while the sex ratio (not significantly different from 1 : 1) of a " sample " (of a single experiment in this case) resembles that of the " population ", and is more or less an accurate index of the sex ratio in the population (the total number of mosquitos bred in the two sets), it differs significantly from that obtained from one set of experiments alone. This is not contrary to expectation since the total figures of neither of the two sets of experiments considered in isolation represent a true " unselected " random sample, the bias at work in the choice of the groups being the predominance of one sex over the other.

The sexes, therefore, emerge in approximately equal numbers collectively, and in isolated samples may exhibit variations which are not statistically significant. This conclusion has been arrived at on the assumption that the two sexes of each brood are exposed to the same ecological conditions. No account has been taken of the mortality occurring either in the larval or the pupal stage and an attempt will now be made to determine the mortality in these stages and to estimate its effect on sex ratio.

Mortality in the Early Stages and its Effect on Sex Ratio.

Out of a total number of 10,023 eggs laid by 70 females, the number of larvae that hatched out was 8,810 (87·8 per cent.) and 7,500 (85·2 per cent.) of these developed into pupae from which 7,165 (95·5 per cent.) adults emerged. The number of eggs laid by a female in the laboratory varied between 56 and 275 and the number laid in nature may also vary considerably.

It is clear that a certain percentage mortality occurs in all stages of development and the point arises as to whether this mortality has any effect on the sex ratio of the emerging adults. Also to what extent the mortality occurring in a particular stage is liable to affect the proportions of the sexes.

Siler, Hall and Hitchens (1926) pointed out that in favourable circumstances males emerge first and in adverse conditions females only emerge, the larvae of that sex being hardier although those of the males are more precocious. If we are to accept this it would imply that larval mortality occurring at any stage, whether early or late, will be at the expense of the male sex only, which does not seem to be probable.

Buxton and Hopkins (1927) state that "As the length of the larval life, especially of the fourth stage, is materially longer for females than for males of both species of *Aëdes*, it follows that any cause of death in the larval stages will produce a differential mortality and kill females rather than males. If, therefore, one wishes to discover the proportions of the two sexes, one must breed from the egg and one can only quote experiments in which the mortality is *nil*, or at any rate very low."

In view of this statement and the observations recorded above that the larval life of females is significantly longer than that of the males, and that there exists no appreciable difference in the egg and pupal durations in the two sexes, it is mainly the larval mortality that would tend to affect sex ratio. But, nevertheless, it should be borne in mind that since it has been shown above that males significantly predominate in the early emergences it is natural that any cause of mortality in the early batches of pupae will definitely affect adversely the total numerical strength of males and in the later emergences that of the females. It is, therefore, suggested that what seems probable is that mortality in the first three larval states affects the two sexes equally ; and in the fourth stage tends to reduce the female numerical strength to a considerable degree ; and that while the pupal mortality in the earlier batches is liable to affect the males adversely, in the later ones it will be mostly at the expense of females, that being the sex which predominates in the later phase.

Although this suggestion seems feasible, it will be seen below that, from a critical analysis of the data furnished in Table IV, it does not apply to a majority of the experiments and its validity comes into question.

Larval mortality.

Out of 70 experiments, larval mortality could not be regularly recorded in five ; a low mortality of below 10 per cent. was observed in 44, in five of which it was nil ; those showing 11 to 20 per cent. mortality were nine and the remainder (11) recorded above 20 per cent. mortality.

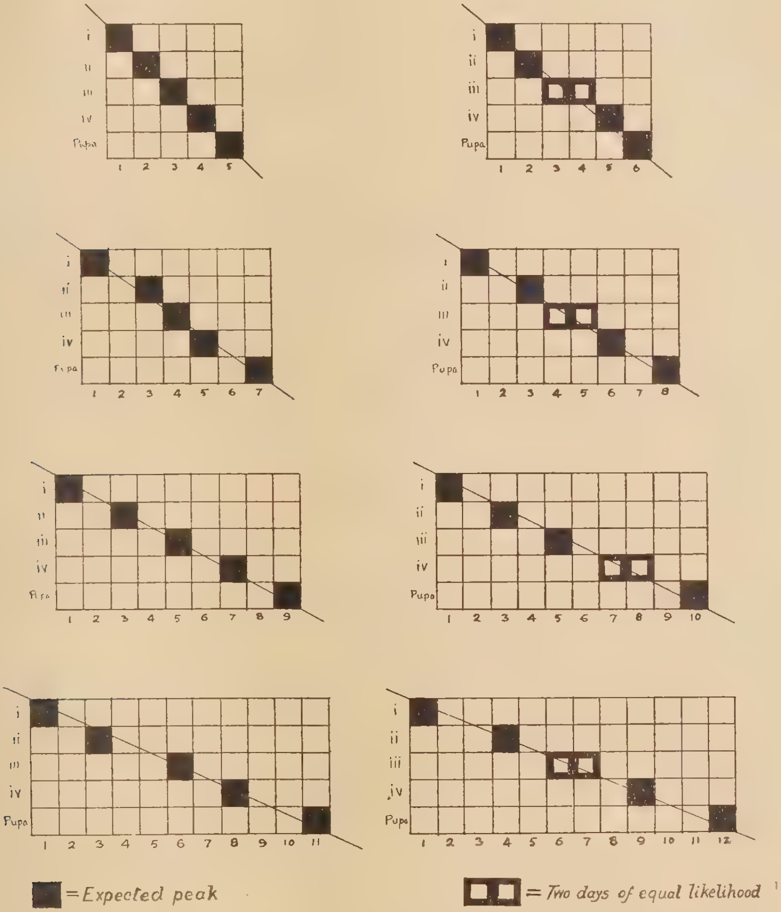
In the 44 experiments in which a mortality of 0 to 10 per cent. was observed, 27 show a male preponderance which is not significant except in three instances, M30, M34 and M37, and 17 experiments exhibit sex ratios in favour of the females that are also not significant except in F6, F11 and F12 (Table II) which will be dealt with later. In the second series of nine experiments which show 11 to 20 per cent. mortality, there are five with a male preponderance and the rest, four, with a favourable female sex ratio.

A more detailed study of the data of the nine experiments reveals that five of the experiments, M13, M20, M22, M23 and M27 with a mortality rate of 14·7 per cent., 16·2 per cent., 11·0 per cent., 17·0 per cent. and 20·0 per cent. have for their sex ratios : 100 : 85 ; 100 : 69 ; 100 : 77 ; 100 : 80 ; and 100 : 69 respectively. None of these ratios have an χ^2 value of P equal to or $<0{\cdot}05$. In the case of the other four experiments, F16, F18, F20 and F28 have mortality rates of 16·0 per cent., 17·6 per cent., 19·0 per cent. and 16·0 per cent. and ratios of male to female of 100 : 106 ; 100 : 121 ; 100 : 113 ; 100 : 102 respectively, which do not depart significantly from 1 : 1 ratio.

The remaining 11 experiments, in which a mortality of above 20·0 per cent. is recorded, merit a closer scrutiny in as much as not only do they show a heavy mortality but also, unlike the foregoing experiments, the mortality figures are not evenly distributed throughout the period of the experiment (Table IV, cols. 2 & 3).

An endeavour was made to keep a careful record of the daily larval and pupal mortality in almost all the experiments by counting the number of larvae while changing the water, and taking account of the pupae while examining the emerging adults. But since all the larvae in an instar did not change into the next stage the same day, it was not possible in all the cases to note down mortality figures for each instar separately. As it was intended to estimate larval mortality occurring in the first three instars taken together on the one hand and in the fourth on the other, these data were recorded as carefully as possible.

To verify these results further, use has been made of Ribbands' (1949) diagrams of theoretical sequence of peaks of the five aquatic stages which are reproduced here (fig. 2) with an addition of the 10-, 11- and 12-day sequences. The first instar and pupal peaks being known, it has been possible to determine with the help of these diagrams the probable date on which the fourth-instar peak occurred, so that mortality occurring before and after this date may be ascertained and its possible effect on sex ratio studied. For example, in experiment M10, since, according to our records, the pupal peak occurs on the tenth day, in order to determine the probable fourth-instar peak, we refer to the 10-day sequence diagram and find that there is a likelihood of its occurrence on the seventh or eighth day. Figures obtained in this way agreed with those actually recorded, especially in short sequences, although in the long sequences there are definite chances of discrepancy and it cannot be entirely depended upon.



Ribbands'[1] *Theoretical Sequences.*

Fig. 2.

Pupal mortality.

In about 85·0 per cent. of the experiments (59 out of 70) a low pupal mortality of 0·0 to 10·0 per cent. was observed ; 33 of these belong to the group with a male preponderance, and 26 to that with a female majority. Between 11 and 20 per cent. pupal mortality was recorded in only five.

It is interesting to note that in 56 experiments (80·0 per cent.) the larval and pupal mortality was below 20·0 per cent. (actually below 10·0 per cent. in an overwhelming majority of cases) and since it is evenly distributed through the period of the experiment it is treated as negligible. A second point of interest which is recorded here with much hesitation and yet deserves close attention and more extensive study is that with a few exceptions heavy pupal mortality is observed in the same experiments that record a high larval death rate. This may be due to the influence of some inherent factor at the time of ovarian development which ultimately leads to higher mortality in the larval and pupal stages. No other cause to which death could be attributed was apparent.

The data in Table IV (compiled from 14 experiments with a high mortality rate, 11 of which are incidentally those referred to in connection with larval mortality) will be taken into account in considering the importance of mortality occurring in the various stages.

M6.—In this experiment the total larval mortality falls in the fourth instar which should, theoretically, result in a male majority in the total output, but it is balanced by a 33·3 per cent. pupal mortality occurring in the earlier batches.

M11.—The larval mortality is evenly distributed and there is a higher mortality (11·1 per cent. in the earlier batches of pupae), than in the later (4·6 per cent.). The significant preponderance of males over females in this experiment cannot be accounted for.

M12.—Out of a high larval mortality of 45·4 per cent., 30·3 per cent. is shared by the first, second and third instars and almost two-thirds of the total pupal deaths (22·0 per cent.) occurred in the earlier emergences, killing thereby a higher percentage of males. The value of P for this experiment is $<0{\cdot}1>0{\cdot}05$.

M14, M16.—Both the experiments show a very heavy pupal mortality taking a heavier toll of pupal life in the earlier batches accompanied by a low larval mortality in all the instars.

M17, M18, M24.—In these experiments, in which a heavy larval mortality is recorded, a higher percentage is shared by the fourth instar and there is a low pupal mortality in the earlier as well as in the later batches. But still, the male preponderance does not depart significantly from 1 : 1 ratio.

M32.—There is a total larval mortality of 50·0 per cent. in this experiment (45·0 per cent. in the fourth instar and 5·0 per cent. in the first, second and third instars). Pupal mortality is nil. It records a significant male majority. This is exactly what theoretically it should be, as a very high larval mortality in the fourth instar may tend to create a male preponderance provided it is not balanced by an unequally high pupal mortality in the early batches.

F4, F10.—These experiments have more or less similar percentages of mortality, *viz.*, a high larval mortality in the fourth instar accompanied by a low overall pupal mortality. Theoretically, these should have shown a male majority, but they record a female preponderance, though not significant.

F11 with a 4·3 per cent. mortality in the first three instars, 2·9 per cent. death rate in the fourth instar coupled with 15·6 per cent. pupal mortality in the early and 6·2 per cent. in the late batches, is an experiment with a significant female predominance.

F13 is a case in which the high larval mortality in the fourth instar is counterbalanced by an almost equally high death rate in the early batches of pupae resulting in the parity of sexes; it shows a female majority though not a significant one.

F14.—In this experiment 43·3 per cent. mortality occurred in the first, second and third instars and 10·9 per cent. in the fourth accompanied by a low pupal mortality. Theoretically, this should have recorded a parity of sexes, if not a male majority ; but it shows a significant female predominance.

Similarly M30, M34 and M37 with a low larval mortality of 2·0 per cent., 0·0 per cent. and 9·2 per cent. show a significant male preponderance.

Again, F6 which shows a low larval and pupal mortality of 5·8 per cent. and 3·5 per cent. exhibits a significant female preponderance.

TABLE IV.

	1	2	3	4	5	6	7	8
S. No.	Experiment	L.M.1 %	L.M.2 %	P.M.1 %	P.M.2 %	S.R. %	P	Remarks.
1.	M6	0·0	23·4	33·3	0·0	100 : 66	0·3	Not significant.
2.	M11	17·5	15·0	11·1	4·6	100 : 50	0·05	*Significant.*
3.	M12	30·3	15·1	14·7	7·3	100 : 53	<0·1>·05	Not significant.
4.	M14	5·8	0·0	27·8	7·2	100 : 80	0·70	Not significant.
5.	M16	8·9	1·4	20·7	14·3	100 : 85	0·70	Not significant.
6.	M17	6·3	28·5	2·2	2·3	100 : 74	0·3	Not significant.
7.	M18	5·0	22·0	1·3	0·0	100 : 80	0·5	Not significant.
8.	M24	4·2	18·5	3·2	0·0	100 : 76	0·5	Not significant.
9.	M32	5·0	45·0	0·0	0·0	100 : 35	0·01	*Significant.*
10.	F4	9·0	12·3	5·6	0·0	100 : 109	0·7	Not significant.
11.	F10	0·0	37·0	3·8	9·9	100 : 214	0·1	Not significant.
12.	F11	4·3	2·9	15·6	6·2	100 : 203	0·02	*Significant.*
13.	F13	5·6	21·9	16·2	2·2	100 : 121	0·7	Not significant.
14.	F14	43·2	10·9	2·9	0·0	100 : 200	0·05	*Significant.*

L.M.1 Larval mortality in first, second, third instars together ; L.M.2 the same in fourth instar ; P.M.1 pupal mortality in earlier batches ; P.M.2 the same in later batches ; S.R. sex ratio ; P value of P for X^2 significance test.

F12 with a 5·0 per cent. mortality in the first three instars and 4·0 per cent. death rate in the fourth instar coupled with 11·4 per cent. pupal mortality in the early and 9·3 per cent. in the late batches shows a significant female preponderance.

The figures for the 14 experiments are too baffling to draw any conclusion in respect of sex ratio and mortality in the aquatic stages, but the validity of the earlier conclusion that sexes emerge in 1 : 1 ratio, based as it is on a considerably larger quantity of data (56 experiments showing low mortality) is unquestionable, though there may exist a small number of cases (M30, M34 and M37 and F6) with a low larval and pupal mortality that show a significant preponderance of one sex over the other.

Effect of Food on Sex Ratio.

The effect of food on the determination of sex in mosquitos has been the subject of study by some workers from both the quantitative and qualitative aspects. Gordon (*l.c.*), thinking it possible that food supply might influence the sexes differently, attempted to breed larvae of *Aëdes aegypti* (L.) (*Stegomyia calopus* (Mg.)) on different quantities of food, other factors being as nearly as possible equal. He found that more males than females hatched when there was a maximum of food available. Berkeley (1902) on the other hand, recorded that the number of males was reduced when abundant food was supplied to the growing larvae. Mehta (1934) working on three different species of *Anopheles* concluded that the quantity of food had no effect on sex ratio. Since this aspect of the problem has not been studied, no light can be thrown on it here.

Endeavour was, however, made to determine the effect of two different types of food on the proportion of sexes, all other factors being kept identical. To this end, two experiments were started simultaneously, the food supplied being yeast in one case and egg powder in the other ; other conditions, including the mean temperature, remained the same for the duration of the experiments.

TABLE V.

Effect of food on sex ratio.

Serial No.	Experiment No.	Food	Mean Temperature ° F	Sex ratio.
A	M12 M13	Yeast Egg powder	84·7 84·8	100 : 53 100 : 85
B	E3 F11	Yeast Egg powder	83·7 83·5	100 : 100 100 : 203
C	F14 F15	Yeast Egg powder	83·9 83·8	100 : 200 100 : 110
D	F16 F17	Yeast Egg powder	87·6 86·6	100 : 106 100 : 133

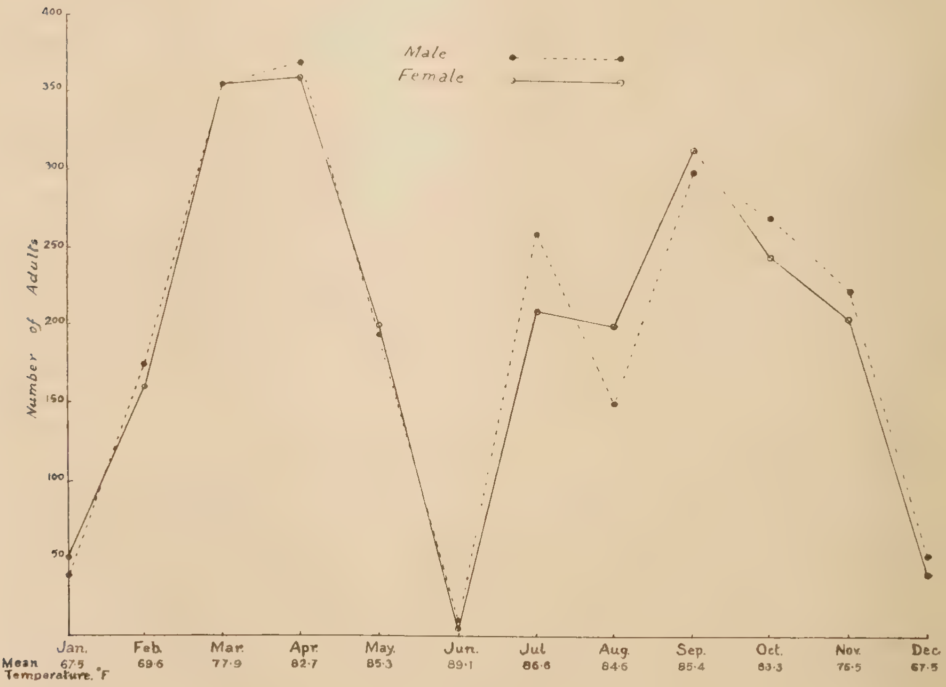


Fig. 3.

The results of four pairs of such experiments are shown in Table III. Proteinous food (egg powder) does not seem to favour the production of males as suggested by Sen (1935) who tried to explain the rise, in Mehta's (*l.c.*) results, from 38 to 46 per cent. males when " water from a natural breeding pool ", which he thought contained protein diet, was substituted for distilled water (yeast being the common food in both), and from 46 to 49 per cent. males when *Spirogyra* was replaced by macerated house-flies as food for the larvae.

Effect of Temperature on Sex Ratio.

The effect of temperature on sex ratio has been studied in two different ways. (1) In fig. 3 an attempt has been made to establish a correlation between monthly mean temperature and the proportion of sexes but it is evident that there does not seem to be any relationship between the rise of temperature and the ratio of the sexes for the month. (2) A second method of studying the effect of mean temperature on sex ratio was to conduct experiments starting on different dates so that the mean temperature for the period of different experiments was the only factor that varied, other factors remaining equal. Figures of mean temperature recorded in the room for each experiment have been set out in Tables I and II but it does not seem to be possible from them to deduce any correlation between the mean temperature and the proportion of sexes.

Discussion.

In discussing the results of these experiments, the question of the order of emergence of the two sexes will be taken first. Rees was perhaps the first worker to have shown that, in captivity, males as a rule hatch out first. Bacot's observations corroborated this view. Gordon also emphasised that males under either favourable or adverse conditions of food emerge earlier than females. Buxton and Hopkins discovered that the larval life for females is longer than for males and hence the earlier emergence of the males, but Mehta in the light of his experiments on Anophelines has not been able to confirm this view and remarks that " no regular order of hatching was observed, either sex emerging first or about the same time."

The results of the present work are in complete agreement with those workers who hold that males hatch out earlier than females. A progressive downward trend in the percentages of males in successive batches of emerging adults has been demonstrated with the help of scatter diagrams. Secondly it has been shown that the percentage of males emerging in the first half of the experiment to the total males is significantly higher in all the 70 experiments. Thirdly, the larval life of females has been proved to be significantly longer than that of males. Mehta has tried to explain his view that no regular order of hatching was observed, either sex emerging first or about the same time by showing that Gordon dealt with mixed batch of eggs whereas he had experimented with the same batch of ova. This argument is not tenable since the results described in this paper are also based on adults reared from separate batches of ova collected from each female separately. It will be seen from Mehta's experiments, however, that in at least three out of eight experiments males have appeared earlier than females. Moreover, a careful scrutiny of his eight charts illustrating the number of males and females emerging daily, reveals that in almost all the cases a larger number of males hatched out in the first half of the experiment than in the second.

While some workers have recorded a favourable male ratio in the emerging adults, others have asserted that either the two sexes hatch in a 1 : 1 ratio or females predominate. Although it appears to be difficult to reconcile these views, a close study of the relevant literature and the results of the present 70 experiments shows :—

(*a*) That since none of the previous workers subjected their data to statistical tests, the genuineness of the occurrence of a majority in one sex or the other is questionable. It is quite possible that the departure from 1 : 1 ratio recorded by these workers may not have been statistically significant as 61 of the 70 present experiments exhibit either a male or female preponderance which is not real.

(*b*) The occurrence of experiments showing a significant majority of one sex or the other indicates that in a small percentage of batches of ova there is a tendency to show either a male or female predominance. But since this is true of either sex and occurs in a small number of experiments only, it can be safely treated as the exception rather than the rule.

(*c*) The proportion of sexes in the emerging adults can only be determined from a large number of experiments ; conclusions arrived at on the basis of insufficient data may prove misleading.

Mortality in the early stages does not seem to cause any disturbance of the equilibrium in the numbers of the two sexes.

Sen's suggestion that a proteinous diet may cause an increase in proportion of males is not supported by the present experiments in which egg powder as the larval food tends to show a lower male numerical strength. It is suspected that food has no effect on sex ratio despite the fact that only a small number of experiments was carried out and that their statistical significance was not tested.

It has also not been possible to establish a correlation between the number of males and increasing temperature.

The writer agrees with Mehta in suggesting that the sexes are determined as early as the ovum, but this does not mean that he also believes that temperature plays no role whatsoever in determining the sexes during ovulation. This must be studied under different constant temperatures in the laboratory before any conclusions can be reached.

Summary.

In view of the great diversity of opinion on the subject of sex ratio and order of emergence of the two sexes of adults in laboratory-bred mosquitos and those occurring in nature, 70 experiments spread over a period of 1 year, were conducted in the laboratory at room temperature to study (*a*) the order of emergence of the sexes, (*b*) proportions of sexes in the total output in a brood, (*c*) the effect of larval and pupal mortality, (*d*) the effect of food, and (*e*) of temperature on sex ratio. The common species, *C. fatigans*, was chosen for the purpose.

By a statistical evaluation and graphical representation of the data it has been shown that males hatch out significantly earlier than females, and that the larval life of the males is significantly shorter than that of the females.

It is concluded that the sexes emerge in a 1 : 1 ratio, although a small number of aberrant cases with a significant preponderance of one sex or the other may occur.

Larval as well as pupal mortality below 20 per cent. does not seem to affect the sex ratio ; nor has it been possible to establish any relationship between sex ratio and mortality in any of the aquatic stages.

Though the effect of food on sex ratio has not been studied extensively, the small number of experiments conducted shows that there is no likelihood of the proportion of the sexes being affected by the different types or the varying quantities of food supplied. [illegible]

The effect of temperature on sex ratio under controlled laboratory conditions has not been specially studied, but it was not possible from the experiments carried

out to deduce any correlation between the mean temperature and the proportion of the sexes.

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STUDIES OF THE RESPONSES OF THE FEMALE *AËDES* MOSQUITO. PART V. THE ROLE OF VISUAL FACTORS.

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(Plate XXI.)

In previous studies of this series, it has been shown that water vapour and carbon dioxide are attractive factors for female *Aëdes aegypti* (L.) (Brown, Sarkaria & Thompson, 1951), and that the warmth of a body is attractive by virtue of the convective effect (Peterson & Brown, 1951). The operation of these factors, all of which are air-borne, has also been demonstrated for the native Canadian *Aëdes* in the field (Brown, 1951*b*).

The purpose of the present study was to evaluate the importance of the visual factors as compared with the air-borne factors already studied. Experiments were confined to black or white surfaces, the question of colour being avoided. Both living and inanimate objects were employed, and the effect of their movement upon their attractiveness was assessed. An evaluation was also made of mirroring effects on surfaces, and of the simultaneous contrast or " contour " offered by black-white interfaces.

Evaluation of the Sight Factor.

The factor of sight as compared with the air-borne factors, in attracting female *Aëdes* mosquitos to bodies, was evaluated by assessing the following :—

(*a*) The attractiveness of a visible body in an airtight container,

(*b*) the attractiveness of a visible body in a perforated container,

(*c*) the ratio of (*b*) to (*a*), as representing the increase in attractiveness due to the air-borne factors, and

(*d*) the comparison of a visible body in an airtight container with an invisible body in a perforated one.

The bodies selected for these experiments were prairie deer-mice (*Peromyscus maniculatus bairdii* H. & K.), which had the grey-brown agouti colour pattern and were slightly larger than laboratory white mice. They were rendered immobile for the required period by anaesthesia with 0·01 grains of Nembutal injected intraperitoneally. They were enclosed in transparent plastic boxes measuring 10 × 5 × 5 ins. These boxes could also be perforated by boring 200 holes ⅛-in. in diameter, or rendered opaque by painting the inside white.

In each experiment a pair of boxes was placed on a white board suspended 4 feet above the floor of the large cage (Brown, Sarkaria & Thompson, 1951), with 24 inches between them (Pl. XXI, fig. 1). The attraction rates were determined by a series of 16 simultaneous pairs of sample counts of the number of mosquitos approaching within 1 inch of each box in 1 minute. As a guide in counting, a white bristol-board card was placed at one end of each box, to protrude 1 inch from the sides and top. To compensate for position and counting errors, the observers were interchanged every four counts and the boxes after eight counts.

Experiment A.—A transparent, airtight, and empty container was compared with a similar plastic box which contained a mouse. Thus the visual response of mosquitos to a dark body could be determined in the absence of any air-borne attractive factors emanating from it.

Experiment B.—A transparent, perforated, empty container was compared with a similar perforated box which contained a mouse. Thus the visual response could be determined in the presence of the air-borne attractive factors such as carbon dioxide, water vapour and convective warmth.

Experiment C.—A transparent, perforated box containing a mouse was compared with a transparent, airtight box, also holding a mouse*. In this way the effect of adding the air-borne factors to the visual factors would be determined.

Experiment D.—An opaque, perforated box containing a mouse was compared with a transparent airtight box, also containing a mouse*. In this way the air-borne factors in the absence of sight could be compared with the visual factors in the absence of the air-borne emanations.

The results in terms of the numbers of mosquitos attracted to each box of the pair tested, and the ratio between them, are shown in Table I.

TABLE I.

Attractiveness to *Aëdes* mosquitos of immobile *Peromyscus* in plastic boxes.
Numbers of mosquitos attracted in 16 1-minute periods.

Experimental Design	Test 1	Test 2	Total	Ratio
A. The Sight Factor : transparent airtight boxes				
Mouse in box	579	918	1,497	1·53
Empty box	391	586	977	
B. The Sight Factor plus Air-borne Factors : transparent perforated boxes				
Mouse in box	860	1,342	2,202	1·58
Empty box	522	867	1,389	
C. Sight plus Air-borne Factors against Sight alone : a mouse in each of two transparent boxes				
Perforated box... ...	1,033	2,037	3,070	1·21
Airtight box	721	1,819	2,540	
D. Sight alone vs. Air-borne Factors alone : a mouse in each of two boxes				
Airtight transparent ...	681	511	1,192	0·73
Perforated opaque ...	951	671	1,622	

The experiments were then repeated, the sole difference being that the mice were not anaesthetised. The normal animal continually paced the floor of the box and occasionally reached up to scratch the lid. The figures, similarly obtained, are summarised in Table II.

These results show that mosquitos can detect the presence of a mouse in an airtight box (see the experiments A), and to a very significant degree if the animal is not immobilised. The presence of a mouse is rendered the more attractive if the box is perforated to allow exit of the air-borne factors (see the experiments B). This enhancement by the air-borne factors is greater when the animal is mobile than when it is anaesthetised (see the experiments B and C). When the animals are mobile the sight factor is more important than the air-borne factors, but when the animals are anaesthetised, it is less important than the air-borne factors (see the experiments D).

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*It was determined by control experiments that there was no significant difference in the attractiveness of the empty boxes *per se*.

TABLE II.

Attractiveness to *Aëdes* mosquitos of normally moving *Peromyscus* in plastic boxes.
Numbers of mosquitos attracted in 16 1-minute periods.

Experimental Design	Test 1	Test 2	Total	Ratio
A. The Sight Factor : transparent airtight boxes				
Mouse in box	538	249	787	3·7
Empty box	150	60	210	
B. The Sight Factor plus Air-borne Factors : transparent perforated boxes				
Mouse in box	500	304	804	6·7
Empty box	75	45	120	
C. Sight plus Air-borne Factors against Sight alone : a mouse in each of two transparent boxes				
Perforated box... ...	435	796	1,231	1·65
Airtight box	328	420	748	
D. Sight alone vs. Air-borne Factors alone : a mouse in each of two boxes				
Airtight transparent ...	908	923	1,831	1·11
Perforated opaque ...	780	864	1,644	

The Factor of Movement.

The effect of the normal movements of the prairie deer-mouse in increasing its visual attractiveness was assessed by the same technique as in the previous experiments. A pair of transparent airtight boxes were used ; one contained an anaesthetised mouse, the other an untreated and normally mobile mouse.

The results of three comparisons, each involving 16 1-minute counts, are shown in Table III.

TABLE III.

The role of movement in host perception.
Numbers of mosquitos approaching a mouse in a transparent, airtight box.

Replication	Active Mouse	Anaesthetised Mouse
1	794	409
2	1,075	643
3	284	164
Total ...	2,153	1,216
Attraction Ratio=1·8		

The figures show that nearly twice as many mosquitos are attracted to a normally moving mouse as to an immobile one.

Investigation was also made of the effect of movement on the attractiveness of inanimate bodies : in this case the body moved in a straight line. A pair of dull black cylindrical canisters, 6 ins. high and 3½ ins. in diameter, were mounted on a board 5 ft. long, at one end of which one canister was immovable while the other was moved to and fro at a rate of 20 ft. per minute (Pl. XXI, fig. 2). Warm moist air was emitted at a rate of 2·5 litres/min. from the tops of each canister, which were covered with black cotton veiling. In each test, 16 paired simultaneous counts were made of the number of mosquitos that touched the veiling in each 1-minute period. Two tests were performed with the canisters. The results are shown in Table IV.

TABLE IV.

Numbers of mosquitos attracted to a moving body as compared with a stationary one.

	Test 1	Test 2	Total	Ratio
Bodies emitting warm moist air at 2·5 litres/min.				
Moving body ...	236	289	525	1·7
Stationary body...	154	151	305	
Bodies with no emission of air				
Moving body ...	112	202	314	1·9
Stationary body...	55	113	168	

The figures show that, with inanimate objects also, nearly twice as many mosquitos are attracted to a moving body as to a stationary one. It was observed that a definite swarm was formed above the moving canister, from which individuals darted to touch the veiling, while other individuals went direct to the veiling without entering the swarm.

Attractiveness of a Mirroring Surface.

The following experiments were designed to investigate the reason for the superior attractiveness of black enamel over a flat black surface observed by Peterson and Brown (1951), which these authors suggested might be due to the mirroring qualities of the enamel.

The Leslie cube, of 10-in. side, was employed in the same way as before. One side was painted with black enamel, and the opposite side with flat black paint ; the adjacent side was painted with a clear lacquer so that the non-mirroring polished metal wall showed through, and to the fourth side was affixed a thin glass mirror. Thermocouple measurements showed the temperature of the black enamel surface to be 32·4°C., that of the flat black surface to be also 32·4°C., while the lacquer surface was 32·2°C. and the mirror 32·1°C. The attractiveness of the black enamel with the flat black surface was compared by means of 16 simultaneous pairs of 1-minute counts, with appropriate changes in positions of the observers and of the Leslie cube, as already described by Peterson and Brown. A similar comparison was made between the lacquered metal surface and the silvered mirror. The results of three sets of these two comparisons are shown in Table V.

TABLE V.

Responses to surfaces on a Leslie cube.
Numbers of mosquitos attracted to within 1 inch of surface.

Replication	Black Paint	Black Enamel	Clear Lacquer	Glass Mirror
1	441	586	393	663
2	616	784	727	1,031
3	269	516	283	476
Totals ...	1,326	1,886	1,403	2,170

The figures show that black enamel is 42 per cent. more attractive than flat black, confirming the results of Peterson and Brown, and that the silvered mirror is 55 per cent. more attractive than the lacquered metal surface. Analysis of the six comparisons by Student's t test gave values of p either less than or slightly greater than 0·001, indicating that the difference was highly significant. Thus in each case the mirroring surface is roughly one-half as attractive again as the non-mirroring surface.

It remained to investigate the way in which a mirroring effect could thus enhance the attractiveness of a black surface. Was it a question of the mosquitos seeing their own reflections, or of perceiving the flicker effect of the reflection of the background behind them ? Therefore tests were made of the effect on attractiveness of affixing 20 pinned mosquitos to the surface, of projecting spots of light or lines of shadow on to the surface, or of causing these projected spots to move across the surface. The spots of light were projected on to the surface by directing a beam from a 35 mm. Kodachrome projector through perforated cardboard held 8 ins. from the surface. The spots were moved by rotating the cardboard at 4 r.p.m. on an axle-rod thrust through its centre. The lines of shadow were produced by placing a cross formed of 2-ft. lengths of 1-in. square wood, painted black, in front of a beam of light. The lines were moved by rotating this cross at 240 r.p.m. on an axle thrust through its centre and located 5 ins. below the beam of light. In all these experiments the assessment was made by comparing the treated surface with an untreated surface similarly illuminated.

The first experiments were performed using dull grey cardboard as the surface. Affixing 20 pinned mosquitos had the effect of raising the attractiveness by 47 per cent., and the difference was highly significant. Removing the mosquitos and leaving the pins only, and placing small squares of black paper on the pins, both had the effect of significantly increasing the attractiveness of the grey cardboard. The projection of spots of light on the surface slightly (but insignificantly) decreased the attractiveness, and the effect of moving these spots of light was a further reduction.

TABLE VI.

Results of experiments to increase the attractiveness of a flat black surface of a Leslie cube. Numbers of mosquitos approaching surfaces with or without treatment.

Treatment	Treated surface	Untreated surface	Enhancement treated/untreated	p Value
20 Pinned adults ...	880 478	901 446	none	—
20 Pins	881 778	870 800	none	—
20 black paper squares	859 1,208	913 1,309	none	—
Stationary light spots	799 1,327	877 1,489	none	—
Moving light spots	873 942	997 1,071	none	—
Stationary shadows	1,263 441	1,228 425	not significant	0·40
Moving shadows ...	1,121 550	842 356	significant	0·001

On the other hand, the projection of lines of shadow caused a slightly significant increase in attractiveness ; when these lines were rapidly swept across the surface, the attractiveness was increased by 32 per cent., and the difference was highly significant.

These experiments were then repeated with a black cardboard surface. A series of 16 simultaneous counts was made on two occasions to assess each treatment. The figures are shown in Table VI. It will be seen that the only treatments to enhance the attractiveness of the black surface were the lines of shadow, and they enhanced it significantly only when they were swept across the surface.

The Factor of Contour.

Starting from the known fact that black is highly attractive to female *Aëdes aegypti*, experiments were conducted with surfaces painted with black in simultaneous contrast to an area of white. These surfaces were placed on wooden cubes of 10 cm. side, and consisted of white kymograph paper painted with black lines or black checks. A cube with such surfaces was compared with a similar cube with a completely black surface, and located 5 ft. from it. Each cube was placed on a white bristol board, and the number of mosquitos approaching within 1 in. of their five exposed sides (total area 500 sq. cm.) was assessed by 16 simultaneous counts, each count terminating when the number attracted to the black standard cube reached 50.

Black lines were used in the first series of experiments. Three cubes were prepared, the first with black lines 1 cm. wide and comprising 125 sq. cm. or one-quarter of the exposed surface, and the second with black lines 2 cm. wide comprising 250 sq. cm. or half the exposed surface ; the third cube was black with white lines 1 cm. wide so that the total area of black was 375 sq. cm. When each cube was compared with the all-black standard cube, they attracted respectively 283, 389 and 648 mosquitos for every 800 attracted by the standard. Thus when the amount of black-white interface or " contour " was kept constant, at 250 cm. total length on the five sides, the attractiveness of the cube increased as the proportion of black to white increased.

Square black checks were used in the second series of experiments. They were alternated with an equal number of unpainted checks of white, so that the total area of black was 250 sq. cm. in all cases. Six cubes were prepared, with checks of side 4·0, 2·0, 1·5, 1·0, 0·75 and 0·5 cms. respectively (Pl. XXI, fig. 3). The checks were so arranged, especially with respect to the junctions of faces, that the total contour lengths were 250, 500, 750, 1,000, 1,500 and 2,000 cms., respectively, for the five exposed sides. The attractiveness of these cubes when compared with the standard black cube is shown in Table VII.

TABLE VII.

Attraction to chequered patterns of various contour lengths.

Dimensions of checks, cm.	Total contour length exposed, cm.	No. of approaches by mosquitos, as compared with 800 for the standard black cube
4·0	250	370
2·0	500	414
1·5	750	456
1·0	1,000	459
0·75	1,500	489
0·5	2,000	563

It is apparent that for a given amount of black on white (250 sq. cm. or 50 : 50), the attractiveness varies directly as the contour length. If these figures are plotted graphically, the position of the 1 per cent. confidence limits on either side is close enough to indicate that the linear relationship is statistically true.

It is also of interest that the attractancy value of 370 for checks at a contour length of 250 cm. and a total black area of 250 sq. cm. compared well with the attractancy value of 389 for lines at a contour length of 250 cms. and a total black area of 250 sq. cm.

Discussion of Results.

These results are in agreement with the conclusion of Kennedy (1940) that *Aëdes aegypti* finds its host through a complex of factors, of which sight is an important one. They tend to show that the visual factors are roughly the equivalent of the air-borne factors in attractiveness under laboratory conditions, the air-borne being the more powerful when the host is still, and the visual being the more powerful when the host is mobile. This is substantiated by our finding that movement nearly doubles the attractiveness of animate or inanimate bodies, which in turn agrees with the discovery of Kennedy that *Aëdes* will orient towards moving black stripes in preference to stationary ones.

The results obtained with the Leslie cube demonstrate that the superior attractiveness of black (or white) enamel surfaces observed by Peterson and Brown (1951) was due, as they had suggested, to the mirror effect. This would result in an increased flicker on the surface as the mosquitos moved up and down the surface, and the reflection of the background they perceived in it would also move. But the experiments showed that it was the moving areas of shadow, not of light, which increased the attractiveness of a black surface on the Leslie cube.

The preference of honey bees for figures that offer the maximum of black-white interface or " contour " has been discovered by Zerrahn (1933), and the reason has been attributed to the greater flicker effect in the pattern of ommatidial stimulation by the more highly contoured objects (Wolf, 1935). Honey bees are phototropic and prefer bright objects to dark ones ; it is therefore of interest that the experiments reported here demonstrate the direct relationship of contour with attractiveness for the mosquito which normally prefers dark objects to bright ones.

Summary.

The role of visual factors in the attractiveness of bodies to adult *A. aegypti* was investigated by exposing deer-mice in transparent or opaque, airtight or perforated, plastic containers. The visual factors proved to be roughly equivalent to the air-borne emanations in attractiveness, being slightly the more attractive when the mice were normally moving, and the less attractive of the two when the mice were motionless.

The attractiveness of a moving black object was found to be nearly twice that of a stationary one. A deer-mouse immobilised by anaesthesia was roughly one-half as attractive as a normally moving one.

Mirroring surfaces are significantly more attractive than dull ones ; a black enamel surface was more attractive than a flat black surface, and a silvered mirror more attractive than a polished metal surface. It was found that enhancement of the attractiveness of a black surface could be obtained by the movement of lines of shadow, not of points of light, across it.

With cubes painted with alternating stripes of black and white, the attractiveness increased with the ratio of black to white. With cubes painted with alternating square checks of black and white, the attractiveness increased as the size of the checks were decreased and the black-white interface or " contour " thus increased, although

the proportion of black to white was equal throughout. For the same proportion of black to white, and for the same amount of black-white " contour ", stripes and checks were equal in attractiveness.

Acknowledgements.

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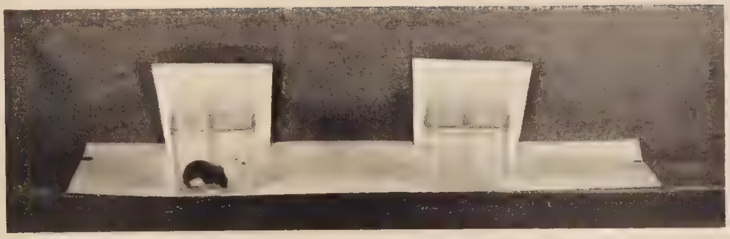

FIG. 1. Example of experiments to assess the importance of visual factors on the attractiveness of bodies for mosquitos. Deer-mice were enclosed in plastic boxes treated in various ways (see text).

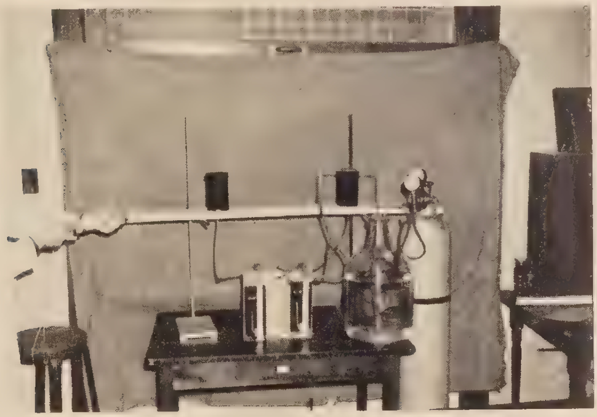

FIG. 2. Apparatus to compare the attractiveness to mosquitos of a moving canister (emitting moist air) with a similar stationary one. The air supply and associated humidifying and flow-rate apparatus were normally kept outside the cage.

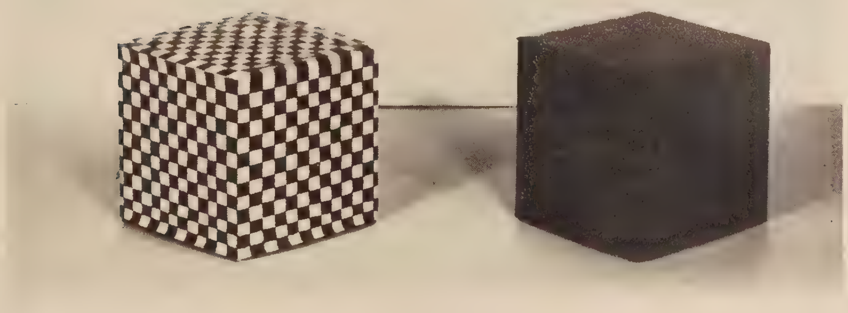

FIG. 3. Examples of 10-cm. cubes, one a black cube used as a standard of comparison, the other with 0·75-cm. checks, for assessment of the effect of contour on attractiveness for mosquitos.

FLIGHT IN DESERT LOCUSTS IN RELATION TO HUMIDITY.

By Z. Waloff.

Anti-Locust Research Centre.

Some recent publications on locust migrations have drawn attention to the great distances which have on occasion been traversed by these insects in single flights, and they have also clearly indicated the greater importance in such cases of air movements in comparison with the locusts' own movements relative to the air (Rainey & Waloff, 1948 ; Rainey, 1951). Moreover, the importance of air movements in determining the direction and the speed of displacement has been shown to apply not only to particular long-range flights, but also to a large-scale movement of swarms characteristic of an area and season (Rainey, 1951). It is clear, however, that any effective displacement of locusts with regard to the ground could not take place unless it were contributed to by active flapping flight or by gliding, and an understanding of the mechanism of locust migrations requires an appreciation of their behaviour and of limiting conditions for flight besides that of the transporting effect of wind (Rainey, *l.c.*).

Of the external conditions affecting flight activity of Desert Locusts, *Schistocerca gregaria* (Forsk.), the limiting low temperatures and the effect of sunshine in lowering the threshold air temperatures for flight have been discussed elsewhere (Waloff & Rainey, 1951) but some recent observations on swarms in East Africa have now drawn attention to another factor which may affect the continuity of flight, and thus the rate of progress, of a migrating swarm.

The flights of locusts can be either continuous, or intermittent, *i.e.*, punctuated by more or less frequent resettling (Waloff & Rainey, 1951). A swarm flying in a sustained manner, with few or no locusts dropping out of the stream and settling, is said to be in continuous flight, while a migrating swarm of intermittently flying

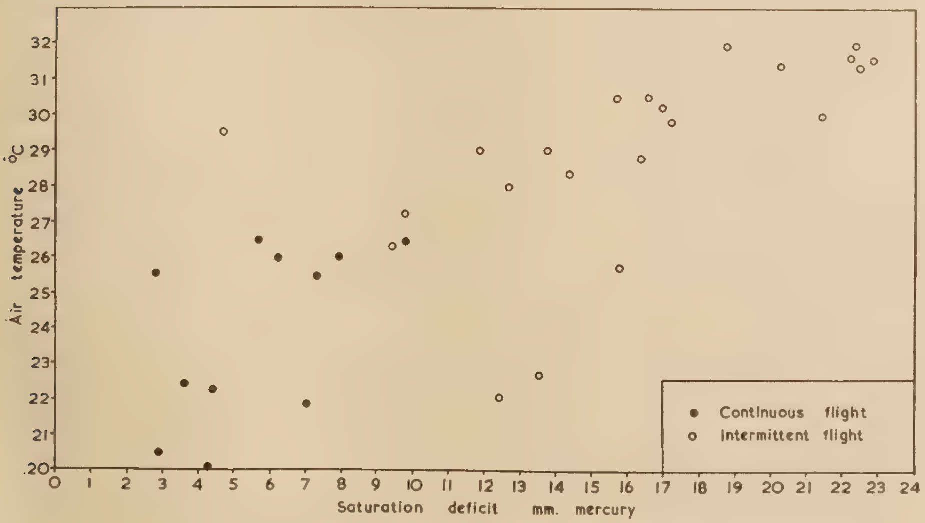

Fig. 1.—Type of flight in Desert Locusts in relation to air temperature and humidity.

locusts is said to roll (Gunn, Perry & others, 1948). Intermittent re-settling, which sometimes may be associated with gusts of wind (Kennedy, 1951 ; Waloff & Rainey, *l.c.*) has been ascribed to a compensatory optomotor response to divergences from a postulated preferred retinal velocity of image-movements over the ventral ommatidia (Kennedy, *l.c.*). The examination, however, of air temperature and humidity conditions (recorded at $4\frac{1}{2}$ ft. above the ground) for 33 cases of migratory flights by swarms of Desert Locusts, observed in East Africa in 1946–47 and 1951, and in Eritrea in 1951*, and comprising 11 cases of continuous and 22 cases of intermittent flight, suggests that other factors apart from optomotor responses are likely to have been involved in the incidence of intermittent flight.

TABLE I.

Type of flight in relation to saturation deficit and air temperature.

Continuous flights n=11

Intermittent flights n=22

	Saturation deficits			χ^2	P(d.f.=2)
	2–8·9 mm.	9–15·9 mm.	16–22·9 mm.		
Continuous flights...	10	1	0	16·53	<0·01
Intermittent flights	1	10	11	8·27	<0·02>0·01
	Air temperatures				
	20–23·9°	24–27·9°	28–32°		
Continuous flights...	5	6	0	5·63	>0·05<0·07
Intermittent flights	2	3	17	19·19	<0·01

All these swarms were seen in sunshine, at mean wind-speeds ranging from 3 to 9 m.p.h. in cases of continuous, and from 5 to 13 m.p.h. in cases of intermittent, flight. Among them, the continuous flights were found to be significantly associated with lower saturation deficits, and intermittent flights with higher saturation deficits (fig. 1 and Table I) ; with regard to air temperatures, the distribution of continuous flights did not differ significantly from random, while intermittent flights showed a significant association with higher air temperatures. The available field data thus suggest that the type of flight performed by locusts may be related to the humidity and possibly temperature of the air ; the evaluation of the respective effects of these two factors is made difficult by the usual high positive correlation between air temperatures and saturation deficits (in this series, $r=0{\cdot}695$, d.f.$=31$, $p<0{\cdot}01$).

There is no evidence from field data that the incidence of flight in swarming locusts is affected directly by the humidity of the air. On the other hand, laboratory investigations by Weis-Fogh (unpublished reports to the Anti-Locust Research Centre) indicate that atmospheric humidity and the water balance in flight have an important effect on flight-performance in suspended locusts flying in a "roundabout" (Krogh & Weis-Fogh, 1952), in which cessation of flight or "truancy" was much more marked at low than at high humidities. It may be suggested, therefore, that the incidence in nature of continuous or intermittent flights may be related to the combined effect of air humidities and temperatures on the water balance of flying locusts.

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* I am greatly indebted to Mr. W. Stower for the Eritrean observation.

Thus, contrary to the earlier views that flight is most active in hot and dry conditions (Ramachandra Rao, 1942 ; Waloff, 1946 ; Kennedy, 1951), it now appears possible that in Desert Locusts the ability to perform continuous flight may be restricted to a relatively limited range of medium to high humidities and moderate air temperatures. Such a limitation would be of special importance during the frequently recorded migrations of Desert Locusts across the sea, when their survival would depend on the ability to continue active flight. In conditions in which maritime modification of the air extends only a short distance above the surface, as for example over the Gulf of Aden during the south-west monsoon or "kharif" season (Meteorological Office, 1944), considerable losses might occur among the high-flying swarms which are often blown out to sea from northern Somali Peninsula by the strong and dry south-westerly winds (Rainey & Waloff, 1948).

The effect of the type of flight on the rate of displacement becomes apparent from the comparison of ground speeds of swarms in continuous and in intermittent flight. In continuous flight the ground speed is the resultant of the wind-velocity and locusts' flying speed and orientation to wind and can be estimated from these data ; it must be noted, however, that such estimates can apply only to the time of the observation, for so far no data are available on the trajectories of such swarms, and it is not known for how long a swarm may remain in continuous flight. In a rolling swarm the ground speed will depend, not only on the triangle of velocities, but also on the mean time per individual locust spent on the vegetation or the ground, and requires for its estimation a knowledge of the trajectory of the swarm over a given period of time. The estimated and observed ground speeds of the available, sufficiently well documented, instances of continuous and intermittent flights are listed in Table II ; all of them refer to low-flying stratiform swarms (Waloff & Rainey, 1951), observed in the course of their diurnal migrations. The trajectories in nos. 11 and 12 were observed from aircraft (Rainey, unpublished) ; in no. 10 the ground speed was obtained by timing the passage of the swarm over a known distance.

TABLE II.

Ground speeds of swarms.

No.	Air temperature °C.	Saturation deficit mm. mercury	Mean wind speed m.p.h.	Approx. mean deviation of orientation from up-wind		
			Continuous flights		Estimated ground speed (to nearest mile)	
1	22·3	4·4	4	0°	5	
2	26·5	5·7	5	20°	5	
3	26·0	7·9	4	30°	6	
4	22·0	7·0	3	45°	7	
5	20·5	2·9	0–3	10°	9–6	
6	26·0	6·2	5	90°	10	
7	22·5	3·6	5	100°	11	
8	25·5	7·3	9	100°	13	
9	26·5	9·8	7	180°	16	
			Intermittent flights		Observed ground speed	Percentage of time spent in effective flight
10	28·8	16·3	8	109°	4 m.p.h.	29
11	31·4	22·5	13	99°	7·8	46
12	29·8	17·1	7	170°	2	12

The estimated air-speeds of Desert Locusts obtained in the field by the mirror technique (Waloff & Rainey, 1951) averaged 7 m.p.h. at 22–24°C., 9·5 m.p.h. at 31°C. and about 11 m.p.h. at 31–32°C. There is no evidence, however, from laboratory investigation of the air-speeds (Weis-Fogh, 1952) that the latter are dependent on air temperature, and a value of 9 m.p.h., which approximates to the mean of the field estimations, was used in calculating the approximate ground-speeds. The percentage of time spent in effective flight was calculated from the proportion of the observed ground-speed to that which might have been achieved, in a similar condition, by continuous flight.

It will be seen from Table II that the very intermittent flights seen in hot and dry conditions may reduce the ground-speeds of stratiform swarms to a fraction of those which could be attained by continuous flight with similar orientations to comparable winds (*cf.* nos. 10 and 8, and 12 and 9), and may cause the swarms to move at a rate well below the speed of wind, even when locusts are flying across or down-wind. It follows that, in some circumstances, the wind speed and the flying speed of locusts play only a subsidiary part in determining the rate of displacement of a swarm, which may depend primarily on the type of flight, and that the frequently made assumption that down-wind flight is faster than up-wind flight (Kennedy, 1951 ; Waloff & Rainey, 1951) does not necessarily apply to intermittent down-wind flights. Further, it now appears probable that the estimated potential air-mileages (Waloff & Rainey, *l.c.*) covered by the " short rains " and the " long rains " generations of swarms in East Africa, where their life-spans include both the wet and the dry seasons, may greatly exceed the air-mileages actually achieved.

It has recently been shown by Rainey (1951) that the displacements of Desert Locusts, which fly at a modest flying speed and apparently without a consistent orientation to wind (Waloff & Rainey, 1951), take place towards, and with, areas of convergent air movement. Further, that during the southward displacement of the Intertropical Convergence Zone across the Somali Peninsula and East Africa in the 1950 " short rains " season, the displacements of the swarms agreed closely with the movement of the Intertropical Front between the advancing surface northerly and retreating southerly winds. The advance of the Intertropical Front was accompanied by widespread showers, and the dates of appearances of the swarms in a series of localities closely followed, or coincided with, the days on which there was rain.

Now although both continuous and intermittent flights have been observed in the course of a rainy season (Waloff & Rainey, 1951), seven out of eleven available records of continuous flight were seen in the Northern Frontier Province of Kenya in the bright intervals between the showers of the 1946 " short rains ", *i.e.*, at the same time of the year and not far from the area in which Rainey (1951) has subsequently demonstrated the striking agreement between the direction and speed of the displacements of the swarms and the movements of the Intertropical Front. On the other hand, on no occasion has continuous flight been seen when conditions were dry, and the very intermittent across- and down-wind flights (Table II, nos. 10, 11, 12), in which the ground speed of the swarms was notably less than the speed of wind, were seen in the Northern Frontier Province of Kenya and in Longido area of northern Tanganyika in February 1951, *i.e.*, during the hot dry season between the " short " and the " long " rains of East Africa (Walter, 1938) when the northern limit of the Intertropical Convergence Zone lay in central Tanganyika ; they refer to instances of the characteristic displacement in that season of the swarms of the " short rains " generation down the prevailing north-easterly winds (Waloff, 1946) blowing towards the Intertropical Convergence Zone.

These observations suggest that the speed of locust displacements might often be higher, and perhaps more closely related to the speed of air movements, in the areas of convergence, where the generally more humid and milder conditions would favour more sustained flight, than when locusts are at some distance from such areas and are traversing hot and dry regions. It has, however, to be noted in this connection that the slow intermittent flights discussed above refer to stratiform swarms flying between the ground and 50–100 ft. above it. Under the influence of thermal convection developing over heated ground, which may be particularly vigorous during the dry seasons, the swarms may sometimes fly in a cumuliform formation, rising to hundreds or thousands of feet above the ground, and with the vertical distribution of locusts appearing to reflect the vertical air movements within the convection cells (Rainey & Waloff, 1951). In a cumuliform swarm, opportunities for resettling would be limited to the times when locusts are near the ground ; moreover, in the thermal up-currents, locusts would remain airborne with less muscular effort than that required for flight in stable air. Again, since in conditions of active convection the temperature of the air up to the altitude reached by convection currents would be decreasing with height at a rate approaching the dry adiabatic, with relative humidities showing a corresponding increase, locusts may encounter more favourable conditions for sustained flight when they are lifted some thousands of feet up in the air, than they would experience near the ground. For example, on the occasion when they were seen from an aircraft at 7,000 ft. above the coast of British Somaliland (10.viii.1946) in conditions indicating that convection currents extended from the ground to at least the height at which the locusts were seen (Rainey & Waloff, 1951), the temperature at 7,000 ft. (recorded by the aircraft) was 22°C., while the presence of fair weather cumulus cloud with bases at 9–10,000 ft. indicated that the saturation deficit at the height of the locusts may have been some 6–9 mm. mercury. The corresponding surface temperature and saturation deficit at Berbera on the coast of British Somaliland were 40°C. and 26 mm.,* and conditions were likely to have been appreciably drier further inland. The effects of drought and heat on the type of flight and the rate of displacement may thus be counteracted at times by the effects of convection, which provides a source of lift and affects the height of flight, and this may account for the recorded association of some notable locust flights during the dry seasons with intense convective activity (Rainey & Waloff, 1951). However, the low intermittent flights referred to above were seen in the presence of vigorous convection, and more information is needed on conditions in which the latter can exercise its full effect.

The question of the rates of displacement of migrating swarms and of their relationship in different conditions and seasons to the speed of air movements appears to require further investigation ; meanwhile the observed effects of humidities and temperatures on the type of flight need to be taken into account in short-range forecasting, for control operations of the probable behaviour of swarms.

Summary.

An analysis of detailed observations on flying swarms of the Desert Locust, *S. gregaria*, on 33 occasions in eastern Africa has demonstrated an association of intermittent flight with higher and of continuous flight with lower saturation deficits. This association, which is consistent with recent laboratory studies on the effects of atmospheric humidity on the flight-performance of suspended locusts, is discussed in relation to the rate of movements of migrating swarms.

Acknowledgements.

I should like to express to Dr. B. P. Uvarov, C.M.G., F.R.S., Director of the Anti-Locust Research Centre, and Mr. P. R. Stephenson, O.B.E., Director of the Desert Locust Survey, my appreciation of their interest during the preparation of this

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* These figures are quoted from unpublished data in the Meteorological Office, by courtesy of the Director.

note, and to Dr. R. C. Rainey and Dr. T. Weis-Fogh for their helpful comments, and for permission to quote unpublished data.

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RESIDUAL EFFECT, SKIN APPLICATION AND INJECTION OF γ-HEXACHLOROCYCLOHEXANE IN *DROSOPHILA MELANOGASTER*.

By D. Dresden and F. J. Oppenoorth.

Panel for research on biocides of the National Council for Agricultural Research T.N.O., Utrecht.

The occurrence of resistant strains is a well-known feature in the practical application of insecticides. There are two important sides to the study of resistant strains; the development of resistance—a genetical problem—and the differences between normal and resistant insects—a physiological problem. It would be of interest to study the *genetical* problems in a resistant strain of *Drosophila melanogaster* Mg., because this insect is genetically so well known and also because of its close relationship to *Musca domestica* L., in which the most outstanding examples of resistance are found. *D. melanogaster* was therefore used in the experiments here described, even though its small proportions are a disadvantage in the study of the *physiological* problems.

As there are physiological investigations in progress at this laboratory on the action of γ-hexachlorocyclohexane, this compound was chosen for the work on resistance. In connection with the study on these genetical and physiological problems the necessity for the evaluation of the two following special experimental procedures arose; a method for the estimation of regression lines, and a technique for the injection of the test insects. The aim of this paper is to give a description of these two procedures.

Material.

The experiments were performed with two strains of *D. melanogaster*, the inbred "Berliner Inzucht" and a mutant: Cy al^2 lt^3 L^4 sp^2; Pm/Cx D; In(3R) Mo Sb. The insects were bred in the usual way in half-pint milk bottles at 25°C. In order to handle them they were sucked into a glass tube by means of a modified "waterpump", differing from its prototype in that air—from the compressed air supply of the laboratory—was driven through it instead of water, thus producing a considerable displacement of air, of which the ordinary waterpump is not capable.

In the contact experiments adults 2–5 days old were used, whereas in the skin-application and injection experiments females of the mutant up to 5 days old, except those just emerged, were used. The mutant for the latter methods was chosen because of its inability to fly, although, of course, in normal flies skin applications and injections are also possible.

Contact Method.

In two of the three methods of application used, namely exposure to a residue, and skin application, the insecticide had to pass through the cuticle. But since the technique of skin application had much in common with the injection method, it will be described with it.

In the technique for contact with a residue, the insects were exposed to the treated surface for 24 hours, which proved to be a suitable period. During this time there must be food available for them. As a result of its presence, however, the walls of the test-tubes in which the experiments were performed became coated with moisture, which introduced the undesirable complication that the insects easily stuck to them. Therefore the insides of the test-tubes were lined with a piece of filter-paper containing a known quantity of poison per sq. cm. (a residue from an acetone solution). At the bottom the piece of food (wrapped in a single thickness of hydrophylic gauze to prevent the insects from sticking to it) was introduced, and the tubes were plugged with cotton wool.

Into each tube 45 to 55 insects were introduced. After a 24-hour exposure (in a dark incubator at 25°C.) the dead were counted. No correction was made for the mortality in the controls (tubes with untreated filter paper), as this mortality was very low.

Skin-application and Injection Methods.

It appeared from preliminary experiments that it is quite possible to administer known doses to the skin of adults, as well as to inject a known quantity of poison. It is indispensable that the insects during these manipulations should be narcotised. Carbon dioxide was used and no mortality was ever found in the controls treated with CO_2 only.

Acetone solutions were used for the skin application, whereas an emulsion was used in the injection experiments. For the latter an emulsion is preferable to lipoids and similar substances, as the latter have the disadvantage of creeping along the injection needle and spreading thence over the cuticle. It should be noted that the emulsions used in these experiments tended to become more toxic when left standing and that they differed in this respect from those mentioned in a previous paper (D. Dresden, thesis 1949, Utrecht).

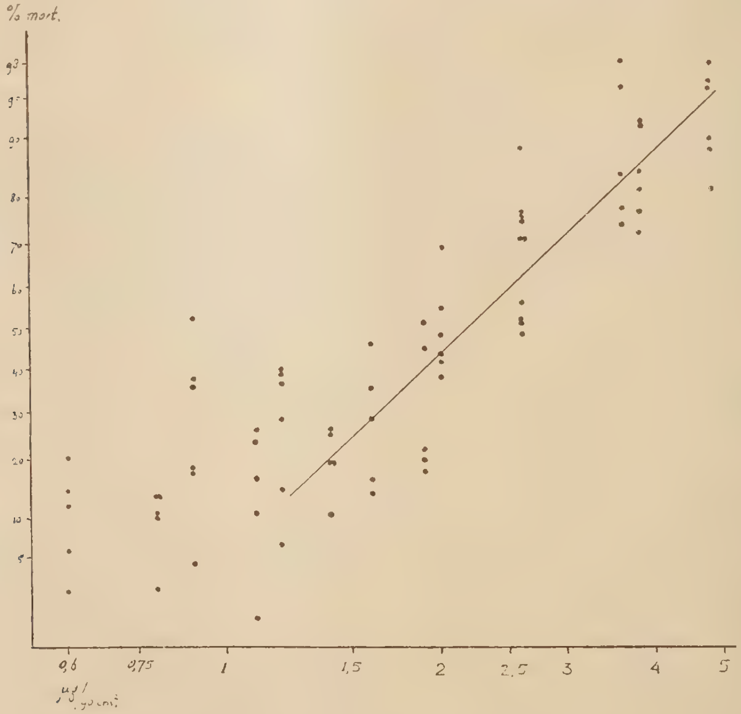

Fig. 1.—" Berliner Inzucht " (" Bi") Contact method. Calculated regression line (see text). Each dot represents ca. 50 flies.

Under a dissecting microscope injections as well as skin applications were carried out with constriction pipettes as used by Linderstrøm-Lang and Holter (Bamann, E. & Myrbäck, K. (1940). Die Methoden der Fermentforschung, pp. 1132–1162, Leipzig, Thieme), the volumes of which were as small as 0·028 and 0·034 μl., respectively. These volumes were estimated colorimetrically.

The pipettes used for injections were of a tip-diameter of about 0·1 mm. The site of injection was somewhere on the lateral part of the thorax, a little dorsally from the halteres. From there the injected fluid spreads easily throughout the body, as can be demonstrated by injections with methylene blue.

The site of the skin applications was the ventral part of the abdomen, only a small area of which was treated with the acetone solution. After treatment the insects were collected in test-tubes, 20 per tube in the case of injections, 25 in the case of skin application. The dead were counted 24 hours later. In the control experiments an emulsion or acetone without the insecticide was applied.

Discussion of the Results.

The data obtained by the contact method, the skin applications and the injections are given in figs. 1, 1a, 2, and 3 respectively. From the following statistical considerations the degree of reliability of the results can be judged.

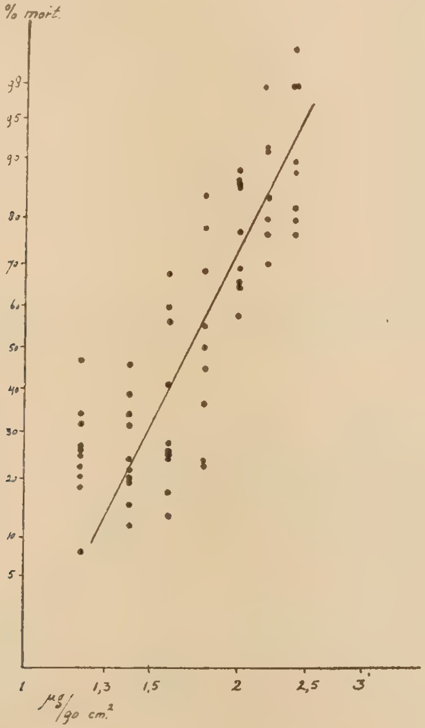

Fig. 1a.—Mutant ("Cy") Contact method. Calculated regression line (see text). Each dot represents ca. 50 flies.

Since the mortality among the controls in the contact and the skin-application experiments was rather small (as a rule less than 3 per cent.), no corrections were applied for these mortalities. In the injection experiments, on the other hand, such corrections could not be avoided as the control mortality was about 13 per cent. in 60 insects.

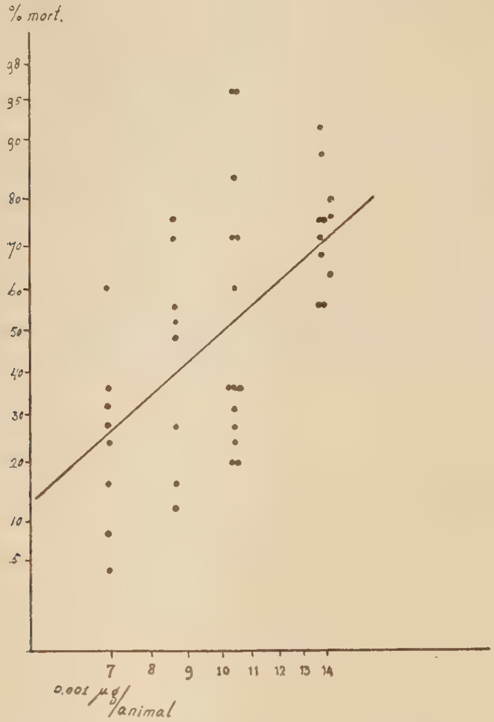

Fig. 2.—Mutant ("Cy") Skin-application method. Calculated regression line (see text). Each dot represents 25 flies.

In general, the replications of experiments with the same dose of poison seemed to show a greater fluctuation than was compatible with random binominal fluctuations. In the contact and the skin-application experiments it was possible, after transformation of the mortality percentages by means of the angular transformation, to show by a χ^2-test that the pooled variances "within doses" greatly exceeded the theoretical variance ($P<0{\cdot}0001$). This may be due to heterogeneity of experimental conditions within the individual test-tubes. In the injection experiments, however, no significant difference between theoretical and experimental variance was found ($P=0{\cdot}34$). Instead of the probit transformation the angular transformation was used for the determination of the regression of mortality on log. dose. In this way the cumbersome weighting at the different doses was avoided. Between mortality 10 per cent. and 90 per cent., the difference between the results of the two methods is quite small.

With the skin-application and the injection methods the regression did not deviate significantly from linearity. The same is true for the contact method if the

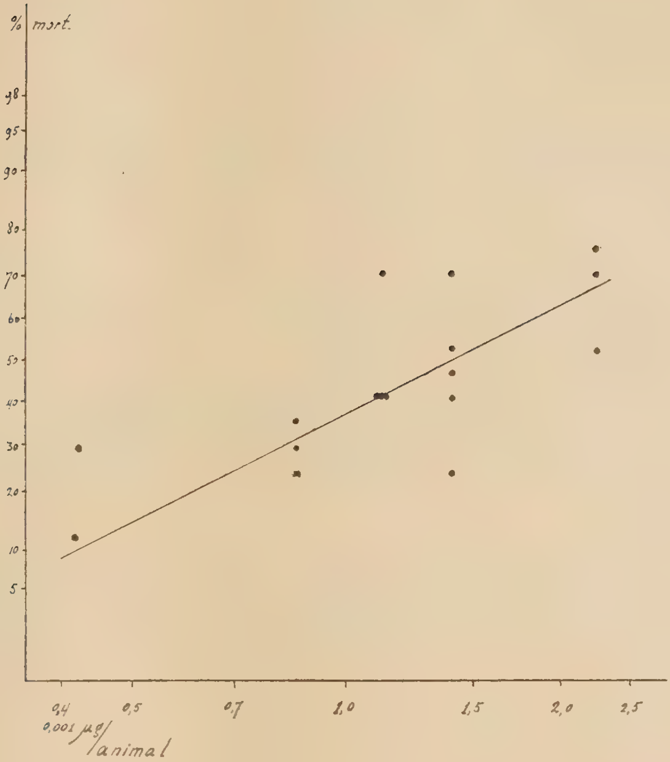

Fig. 3.—Mutant ("Cy") Injection method. Calculated regression line (see text). Each dot represents 20 flies

results obtained with doses smaller than 1·25 µg. γ BHC are not taken into consideration.

The confidence interval for the LD50 was calculated by means of Fieller's formula (Quart. J. Pharm., **17,** 1944, pp. 117–123). The results were :—

Experiment	Conf. int. LD50	Mean LD50
Contact method "Cy" ...	1·65–1·76 µg. γ BHC	1·71 µg. γ BHC
Contact method "Bi" ...	2·04–2·31 µg. γ BHC	2·18 µg. γ BHC
Skin application "Cy" ...	0·0086–0·0113 µg. γ BHC/ insect	0·0099 µg. γ BHC/insect
Injection "Cy"	0·00115–0·00190 µg. γ BHC/ insect	0·00141 µg. γ BHC/insect

It is remarkable that the LD50 after injection is only one seventh of the LD50 after skin application, for it is generally assumed that γ-hexachlorocyclohexane penetrates very easily and almost quantitatively through the insect cuticle. It might be objected that the low LD50 after injection was caused by an injurious effect of the injections as such. Consequently some individuals were injected with the control emulsion and at the same time the poison was applied to the skin, whereas in another group of insects only skin application was carried out. Within reasonable limits, the mortality in both groups appeared to be the same.

Summary.

As a basis for future investigations on the development and the nature of resistance against insecticides, the regression lines for the toxicity of γ-hexachlorocyclohexane to *D. melanogaster* were estimated by means of:

1. A contact method, in which the insects (adults) were exposed to a treated surface.
2. A skin-application method, in which measured doses of an acetone solution of the poison were used.
3. An injection method in which adults were injected with known doses of an emulsion containing the insecticide.

The reproducibility of the results obtained with the above methods is briefly discussed. It was found that in the case of the skin-application and injection methods the regression line did not deviate significantly from linearity. The same was true for the contact method if the results obtained with the smaller doses were not taken into consideration.

Acknowledgements.

The authors are indebted to Dr. E. F. Drion of the Statistics Department T.N.O. for his inestimable help in the statistical analysis of the data.

A NOTE ON THE PREPUPAL STAGE AND THE EXTERNAL SEX CHARACTERS OF THE PUPAE OF *ANOBIUM PUNCTATUM* (DEG.) (COLEOPTERA, ANOBIIDAE).

By J. D. Bletchly, B.A., B.Sc., F.R.E.S.

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External characters enabling the sexes to be distinguished readily in the adult *Anobium punctatum* (Deg.), popularly known as the common furniture beetle, have been described by Kelsey & others (1945) but no account has yet been published of the external sex characters of the pupae of this Anobiid. In the course of research at the Forest Products Research Laboratory on the biology of this species, a series of larvae in the prepupal stage and of pupae have been examined to determine whether the sexes can easily be recognised in the immature stages. Sex determination, before the adult stage is reached, is of great value for experimental work on breeding techniques and other projects.

Prepupal Stage.

Prior to pupation the curved scarabaeoid eruciform larvae straighten and specimens at this stage were obtained from hazel wattle fencing (*Corylus avellana*). This fencing had become infested out-of-doors and had been kept subsequently in an outside insectary at the Laboratory. The prepupae were weighed individually, kept separately in labelled tubes in the insectary and reared through the pupal stage to the adult in order that the sexes could be determined. In this way a series of weights for the prepupal stages of both sexes was obtained (Table I).

TABLE I.
Weights of prepupae.

Males	Females
2·3 mg.	2·7 mg.
2·6 ,,	2·9 ,,
2·9 ,,	3·1 ,,
3·1 ,,	4·7 ,,
3·1 ,,	4·7 ,,
3·6 ,,	4·9 ,,
4·1 ,,	4·9 ,,
4·2 ,,	5·1 ,,
4·3 ,,	5·2 ,,
4·8 ,,	5·3 ,,
5·6 ,,	5·7 ,,
5·9 ,,	6·0 ,,
	6·4 ,,
	8·6 ,,
Average 3·9 mg.	Average 5·0 mg.

In addition, two prepupae, which died before they fully pupated and whose sex could not, therefore, be confirmed but which appeared to be male, weighed 8·8 mg. and 9·2 mg. and were thus heavier than any of the females weighed in this series. If the weights of these two specimens are included in the above table the average male weight becomes 4·61 mg., which is little lower than that for the average female.

If the " t " test (Brownlee, 1949) is applied to the average weights given in Table I, the difference is significant at the 5 per cent. level, but if the weights of the two specimens whose sex was in doubt are included in the data for males, the averages then obtained are not significantly different. It is apparent, therefore, that the females cannot be accurately separated at this stage on a weight basis. The great variation in weights of both sexes and the low weights at which pupation can occur are noteworthy. Becker (1942) stated that the largest larvae weigh 13–14 mg., but that pupation may occur after a weight of 3 mg. is reached. It must be pointed out that the figures in Table I relate only to those individuals taken from the environment described and a study of the factors governing pupation did not form part of this investigation.

External Sex Characters of the Pupae.

The pupae bear a superficial resemblance to those of the death-watch beetle, *Xestobium rufovillosum* (Deg.), as described by Fisher (1937), and of the drug store beetle, *Sitodrepa panicea* (L.) as described by Metcalfe (1932), but differ considerably in the appearance of the external sex organs.

The female (fig. 1) is, on the average, larger and heavier than the male. The prepupae whose weights are given in Table I, were not weighed again after pupation, but other pupae obtained from a different source—alder ply with blood glue also kept under out-of-door conditions—were weighed and it was found that the average weights of 19 males and 25 females were 2·4 mg. and 3·8 mg. respectively. The female is more pointed posteriorly but a reliable character for distinguishing between the sexes at the pupal stage and visible to the naked eye, is the presence of a pair of processes corresponding to the genital appendages of the female pupae of *Sitodrepa* and *Xestobium*. As in the latter, these processes, which project considerably beyond the last sternite, are symmetrical and consist of two segments only, whereas in *Sitodrepa* the presence of an additional segment on one side produces asymmetry (Metcalfe, 1932). The gonopore, as in the other two Anobiids mentioned, is situated between the bases of these appendages. A sub-circular depression with a median furrow in the centre of the eighth sternite and a crescent-shaped depression in the seventh correspond closely to those described in the death-watch beetle by Fisher. It is possible that invaginations which give rise to the formation of the uterus and chitinous rod of the adult female reproductive system, which are discussed in Metcalfe's paper, arise in these depressions respectively, and, in this case, the gonopore would correspond to the spermathecal invagination. Further embryological work is needed to confirm this suggested interpretation.

In the male (fig. 1), there is a pair of symmetrical processes on the last sternite, each consisting of a single segment, and connected together at their bases by a protuberant strip. These processes appear to resemble the " conical processes " of *Xestobium* and to correspond to the lateral lobes of *Sitodrepa*, but the asymmetry described by Metcalfe in the latter does not occur. This absence of asymmetry in *Anobium* is of interest since both Pic (1912) and Böving (1927) include this genus in the same group as *Sitodrepa* in which the somewhat asymmetrical appearance of the median lobe is apparently due to incomplete separation from the left lateral lobe during ontogeny (Metcalfe). On the other hand, these authors place *Xestobium* in a separate group and the greater degree of asymmetry in this species supports their views. In the females, however, a converse asymmetrical condition is present since it is found in *Sitodrepa* unlike *Xestobium* and *Anobium*. Between these lobes a somewhat heart-shaped structure represents the median lobe of *Sitodrepa* and the two small asymmetrical tubercles in *Xestobium*. The small unpaired median papilla illustrated by Fisher in *Xestobium*, appears to be represented by a minute median process on the protuberant strip connecting the two symmetrical processes distinguishable only after fixing and clearing. The bilobed processes noted by Fisher in *Xestobium* are probably represented by a semicircular strip anterior to the lateral lobes, which corresponds to the telson of the adult (Kelsey & others, 1945). Like *Xestobium*, the sub-circular depression on the eighth sternite of the female is absent and the crescent-shaped depression on the seventh, although present, is less marked than in the female. It is difficult to interpret the significance of this depression. On the basis of a comparison with Metcalfe's description of *Sitodrepa*, where it appears to be absent, it seems that none of the internal reproductive structures originates as an invagination of the seventh sternite. It is possible, therefore, that the distinct crescent-shaped depression of the female has a somewhat vestigial representative in the male. The depression on the last visible sternite (probably the eighth) of the adult male described by Kelsey & others (1945) is not represented in the pupa.

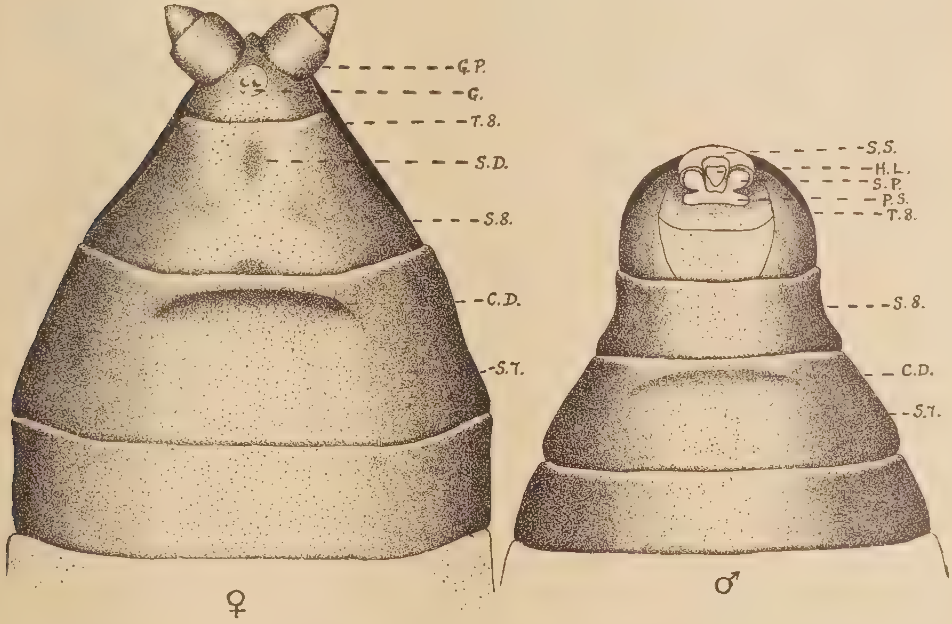

Fig. 1.—*Anobium punctatum*. Ventral view of distal segments of pupa. C.D., crescent-shaped depression ; G., gonopore ; G.P., genital process ; H.L., heart-shaped lobe ; P.S., protuberant strip ; S.7., sternite 7 ; S.8., sternite 8 ; S.D., sub-circular depression ; S.P., symmetrical process ; S.S., semi-circular strip ; T.8., tergite 8.

Acknowledgements.

The work described above has been carried out as part of the programme of the Forest Products Research Board and is published by permission of the Department of Scientific and Industrial Research. The author wishes to record his thanks to Dr. R. C. Fisher, Officer-in-Charge of the Entomology Section, for helpful criticism of this manuscript, and to Miss S. Simpkin for preparing the original pencil drawings for publication.

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STUDIES OF BRITISH ANTHOMYIID FLIES.

By Mary Miles.

Wye College, University of London.

(Plate XXII.)

IV. Biology of the Spinach Stem Fly, *Hylemyia echinata* (Séguy).

Spinach (*Spinacia oleracea*) is grown in the east and south of England for processing and processers have been aware for some time that the crop was subject to infestation by maggots. The nature of the attack and the identity of the maggots were not known because the insects were found only when the crop was being processed. The examination of maggots from partly processed material from the east of England showed that they differed from those of species previously recorded from spinach : the Mangold Fly (*Pegomyia betae* (Curt.)), the Bean Seed Fly (*Delia cilicrura* (Rond.)) and a saprophytic species (*Pegohylemyia fugax* (Mg.)).

In 1950 I had an opportunity to examine spinach grown for seed at Wye, Kent, and was able to collect a small number of larvae similar to those from processed spinach. Flies reared from them were identified by Dr. F. I. van Emden (Commonwealth Institute of Entomology) as *Hylemyia echinata* (Séguy), a species hitherto unknown in the literature of economic entomology. In the late summer spinach was again sown on the same field and *H. echinata* was again found on the crop. From this it was concluded that the species was established in the district.

In April 1951 spinach was sown on an observation plot about half a mile from the site where *H. echinata* had been found in the previous year. The seedlings were examined daily for the occurrence of eggs and larvae. In the latter part of May unknown eggs were found on the leaves and when the larvae hatched they were recognised as those of *H. echinata*. Observations were then made on the life-history and habits of the species.

Eggs.

The eggs (Pl. XXII, fig. 1) are approximately 0·9 mm. long, white, elongate, with one side rather flattened. The anterior end is truncate with a thick rim from which a pair of ribs extend along the flattened side for about a quarter of the length of the egg. The posterior end is rounded. The chorion has broken longitudinal ridges similar in appearance to those of eggs of the Cabbage Root Fly (*Erioischia brassicae* (Bch.)), but eggs of *H. echinata* can be readily distinguished from those of *E. brassicae* by the length of the ribs which in the latter species extend from end to end.

The eggs are laid singly on the upper sides of young leaves, usually in the troughs formed by the veins. They may also be found among the opening leaf buds and in the leaf axils. They do not adhere to the leaves and may be dislodged by heavy rain.

The incubation period varied with the temperature and lasted 2–4 days in the laboratory.

Eggs of *H. echinata* can be easily distinguished from those of other Anthomyiid flies that occur on spinach. Eggs of *P. betae* are laid on the under sides of the leaves, usually several in a row, and their surface is coarsely reticulated (Pl. XXII, fig. 2) ; they adhere closely to the leaves and cannot be removed without damage. Eggs of

P. fugax are laid indiscriminately on the upper and lower surfaces of the leaves, and can be recognised by the irregular keeled ribs which extend the full length of the eggs and large rounded reticulations of the chorion (Miles, 1952). I have not found eggs of *D. cilicrura* on spinach in Kent but should they occur it should be possible to recognise them from recorded descriptions (Miles, 1952).

Larvae.

Habits.—The larvae rupture the chorion of the egg between the ribs at the anterior end and emerge on the upper surface of the leaves. The feeding site is the inner surface of a hollow mid-rib, petiole or stem, but they do not always find it immediately. They may wander a short distance before tunnelling into the mesophyll and they may make a small blotch mine before reaching the mid-rib. Sometimes they make an irregular linear mine along the edge of a lateral vein which serves as a guide to the mid-rib. Larvae from eggs laid on terminal or axillary buds feed on the leaf tissue as they tunnel towards the stem.

The habits of larvae of *H. echinata* are so different from those of larvae of *P. betae* that the two species should not be confused. Larvae of *P. betae* escape from beneath the eggs and tunnel directly into the leaf tissue. They do not wander on the surface, indeed, they seem incapable of penetrating the leaf epidermis except where the eggs are gummed to it, and for some time after hatching they can be seen in the mesophyll feeding together in a row. As they develop they produce large conspicuous blotch mines in which the larvae become scattered. They are not found in the mid-ribs or petioles.

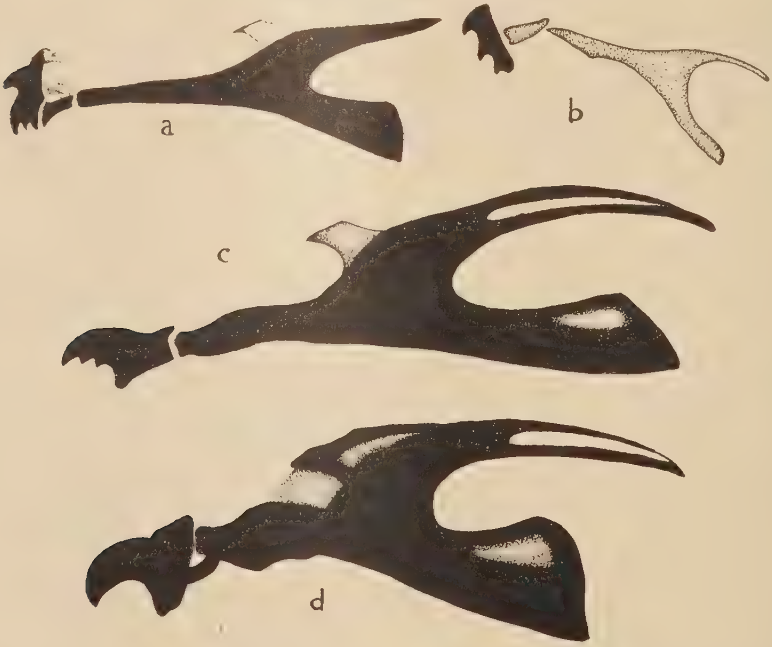

Fig. 1.—Bucco-pharyngeal armature of : a, first instar of *H. echinata* (× 200) ; b, first instar of *P. betae* (× 150) ; c, second instar of *H. echinata* (× 200) ; d, third instar of *H. echinata* (× 100).

Description.—Larvae of *H. echinata* attain a length of 6–7 mm. when fully grown and resemble larvae of *E. brassicae* in general form (Miles, 1952). The head is small and retracted into the broad prothorax. The lateral lobes carrying the antennae and maxillary palps are small and inconspicuous. The antenna consists of a densely sclerotised basal ring and a spherical terminal segment. The maxillary palp consists of a densely sclerotised ring with several papillae, two of which are more heavily sclerotised than the rest.

Diagrams of the buccal armature of the three larval instars are given. In the first instar (fig. 1 *a*) each mandible consists of a single sclerite with two large teeth and two small teeth, the posterior of the small teeth being the ventral process. The form of the two large anterior teeth suggests that they may have had a similar origin to that of the two separate oral crotchets of *E. brassicae* (Miles, 1952). A comparison of the mandible of the first instar of *H. echinata* with that of the first instar of *P. betae*, which is also used to rupture the epidermis of spinach leaves, shows that in both species it consists of a single sclerite, but in *P. betae* (fig. 1 *b*) the teeth are arranged in a straight line while in *H. echinata* they are arranged round an angle. In the second and third instars the mandibles of *H. echinata* are similar in form to those of the same instars of *E. brassicae*. In the second instar (fig. 1 *c*) they are stout and strong with two subsidiary teeth and with no accessory sclerites. In the third instar (fig. 1 *d*) the mandibles are simple hooks, short, stout and heavily sclerotised.

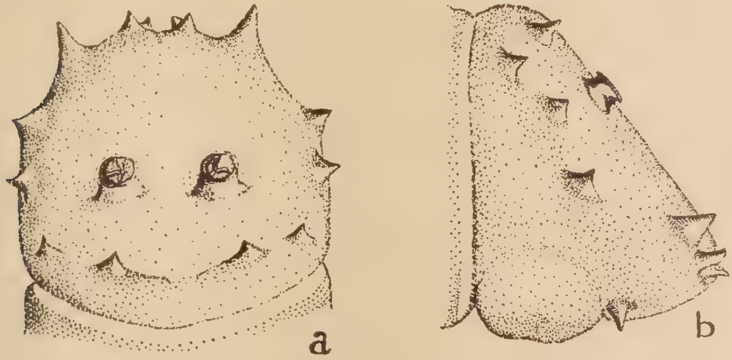

Fig. 2.—*H. echinata*, 8th abdominal segment, third-instar larva (× 46), *a*, dorsal view; *b*, lateral view.

The anterior spiracles have six or seven finger-like processes. The posterior spiracles are small fleshy knobs projecting slightly from the dorsal oblique area of the eighth abdominal segment. The edges of the spiracular slits, the moulting scars and the peritremes of the spiracles are lightly sclerotised.

The tubercle pattern of the eighth abdominal segment (figs. 2, 3) differs from that of other Anthomyiid larvae so far studied. The tubercles are uniformly small and subconical except for the outer apical tubercles which are much larger than the rest. There are no bifid tubercles but the base of each inner apical tubercle is almost contiguous with that of the corresponding ventro-apical tubercle.

Larvae of *H. echinata* from spinach are characteristically ringed with black (Pl. XXII, fig. 3). This discoloration is superficial and is caused by the coagulation of sap among the minute spicules of the integument. Larvae of *P. betae* do not show similar discoloration.

Puparia.

Puparia are usually found in the soil but sometimes they are formed in the feeding tunnels. They are 4–5 mm. long, brown and oval. The head and prothorax are retracted and the anterior spiracles project conspicuously. The thorax is flattened dorso-ventrally and splits along the lateral folds when the fly emerges. The tubercle pattern of the eighth abdominal segment is clearly visible on the puparium and can be used for identification.

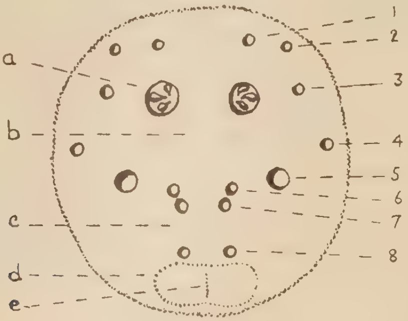

Fig. 3.—*H. echinata.* Diagram of 8th abdominal segment (hind view) *a*, posterior spiracles ; *b*, dorsal oblique area ; *c*, ventral truncate area ; *d*, 9th abdominal segment ; *e*, anus. Tubercles : 1, dorso-central ; 2, dorsal ; 3, dorso-lateral ; 4, lateral ; 5, outer apical ; 6, inner apical ; 7, ventro-apical ; 8, supra-anal.

Adults.

Representative specimens were identified by Dr. F. I. van Emden as *Hylemyia echinata* (Séguy). Males have been described by Séguy (1923).

The flies are 4–5 mm. long, yellowish-grey with black legs and an indistinct dark median stripe on the thorax and abdomen. The wings are clear and iridescent with the nervures yellow at the base, the squamae are equal and pale yellow, and the halteres yellow.

The head is sub-triangular in profile. The eyes are devoid of hairs, and are close together in the males and separated by a broad frontal band in the females. The orbits are pale silvery grey and a yellowish or brownish area extends from the lunule towards the ocellar triangle. The antennae are black and the arista has short fine pubescence. The palps are slender, black and clavate.

The thorax has short fine acrostical bristles with the second presutural pair longer and stronger than the rest. The pre-alary bristle is short but quite distinct. In the males the sternopleural bristles, one in front and two behind, are long and strong but in the females the lower hind sternopleural bristle is short. The tibiae of the mesothoracic legs have no antero-ventral bristles but have one antero-dorsal bristle and usually only one postero-dorsal bristle. Specific characters occur on the hind tibiae of the males which have two to three antero-ventral bristles, five to six antero-dorsal bristles, three dorsal bristles and two to three fine postero-ventral bristles near the base. The chaetotaxy of the hind tibiae of the females does not provide specific characters.

In the males the abdomen is strap-like. In both sexes the abdominal segments have dark median areas which form a broken longitudinal stripe, and in the males the areas extend laterally to form transverse bands. The males have a few long, strong backward-pointing bristles on the third sternite which pass through a tuft of rather fine erect bristles on the fourth sternite.

Females of *H. echinata* closely resemble those of *D. cilicrura* and *D. trichodactyla* (Rond.) from which they cannot be distinguished by means of Karl's key. I am indebted to Dr. van Emden for the suggestion that differences between *H. echinata* and the *D. cilicrura-trichodactyla* complex should be sought in the occurrence of small setae behind the post-orbital bristles. In *H. echinata* there is a slightly irregular row of 6–8 small setae beginning behind the vertical setae and extending in a nearly parallel line behind the post-orbital setae ; the second row is shorter and more widely spaced than the first (fig. 4). A second row of post-orbital setae does not occur on *D. cilicrura* and *D. trichodactyla* though 1–2 setae may be present.

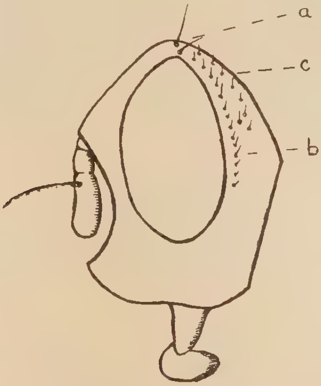

Fig. 4.—Diagram of head of *H. echinata* (♀) showing position of two rows of post-orbital setae. a, vertical setae ; b, post-orbital setae ; c, second row of post-orbital setae.

Annual Cycle of Generations.

H. echinata has three to four generations a year. In 1950 and 1951 larvae were first found in May and were present on the food-plants until late September. The second generation of flies emerged in late June and early July and in captivity further emergences occurred in August and September. From these observations it appears that in suitable weather *H. echinata*, like *E. brassicae* and *D. cilicrura*, is active from April to October.

Economic Status.

I have found *H. echinata* to be phytophagous on *Spinacia oleracea* but it is probable that it has other food-plants because in 1950 it was taken on a first crop of spinach in a field far from gardens and allotments. Séguy (1923) states that it is a parasite of *Tortrix rigana* (Sodovsky) but gives no supporting evidence.

The injury to spinach is not conspicuous. Infested leaves show a small discoloured blotch where the larvae enter the tissue and the mid-rib may bend sharply backwards to a right-angle with a small brown area in the angle on the under side. Attacked petioles later split and reveal the blackened feeding tunnels of the larvae (Pl. XXII, fig. 4). When the larvae feed in the buds the unfolding leaves are ragged and imperfect with the bitten edges black. The stems of attacked shoots are deformed and blackened by larvae feeding for a time on the surface before they penetrate the tissue.

The nature of the spinach crop as grown for processing makes control of *H. echinata* difficult. Seed is drilled in April and practically the whole plant is cut for harvest early in June. The crop is therefore exposed to attack by the first generation of flies but any protective treatment with sprays or dusts is likely to contaminate or taint the foliage.

The severity of attack depends on the length of time that elapses between the spring peak of egg-laying and the date of harvesting the crop. The present limited observations suggest that *H. echinata* responds to weather conditions in the same manner as the related species, *E. brassicae* (Miles, 1951), and that the risk of severe attack is greatest when spring is early. In such seasons it may be advisable to harvest the crop before it has made its full growth in order to limit the extent of infestation.

It seems probable that *H. echinata* is widely distributed. Séguy records it from the neighbourhood of Paris and Karl states that it is not uncommon at Stolp (Germany). It has occurred in sufficient numbers on spinach in the east of England to attract attention, and growers in east Kent are aware of its occurrence on local crops. I found it at Wye on the first field crop of spinach I was able to examine and have received specimens from spinach grown on the Weald. I have also seen the injury on spinach from a garden near Bristol.

Acknowledgements.

Thanks are due to the Principal and Governors of Wye College who have provided facilities for the investigation. The help of Prof. Herbert W. Miles in the conduct of the work and the preparation of illustrations is gratefully acknowledged. Dr. H. C. Gough, Adviser in Entomology to the Cambridge Province (N.A.A.S.), first drew my attention to the occurrence of *H. echinata*.

Summary.

The Spinach Stem Fly *Hylemyia echinata* (Séguy), is an important pest of spinach (*Spinacia oleracea*) grown in the east and south-east of England for canning and freezing. Attack by the larvae results in the blackening and distortion of terminal shoots and the splitting and discoloration of petioles and mid-ribs, and some larvae may be present in the crops when they are harvested.

The eggs are laid in May on the upper surfaces of the leaves and among the leaflets of the terminal and axillary buds. The larvae penetrate the epidermis and tunnel through the mesophyll until they reach mid-ribs, petioles or stems where they feed on the hollow inner surfaces. The puparia are usually found in the soil but may occur in the feeding sites. The second generation emerges in June and July, and further emergences occur in August and September. Larvae are present in the crops from May to October.

Eggs and larvae are described and illustrated so that they can be distinguished from those of the Mangold Fly, *Pegomyia betae* (Curt.), which are often present on spinach at the same time. The flies are described and the characters which distinguish them from the Bean Seed Flies, *Delia cilicrura* (Rond.), are noted.

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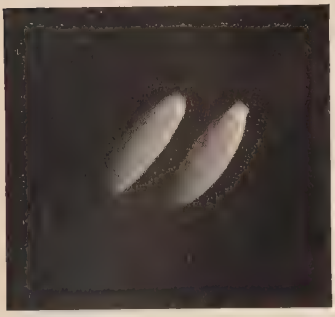

FIG. 1. Eggs of *H. echinata*. (X 20).

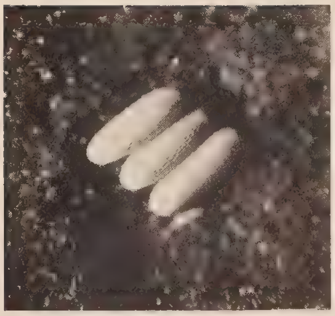

FIG. 2. Eggs of *P. betae*. (X 18).

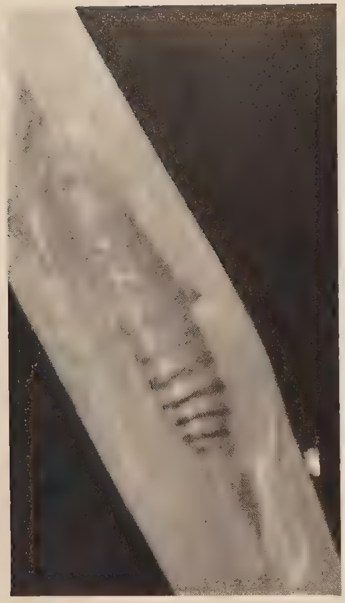

FIG. 3. Third instar larva of *H. echinata* as it appears in its feeding site.

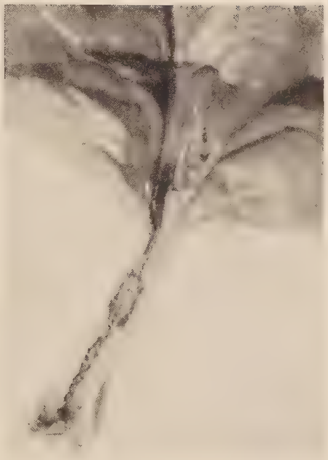

FIG. 4. Damage to petiole of spinach leaf by larva of *H. echinata*.

SIMULIUM DAMNOSUM AND ITS RELATION TO ONCHOCERCIASIS IN THE ANGLO-EGYPTIAN SUDAN.

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(Plate XXIII.)

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The Simuliid fauna of the Sudan was described by Lewis (1948, 1952), and the present paper records work on *Simulium damnosum* Theo. which was largely carried out during two expeditions to Mvolo (Lat. 6° 03′N., Long. 29° 56′E.) and other onchocerciasis areas (see fig. 2) from May to July 1948 and August to November 1949.

The internal organs of S. *damnosum* were studied in relation to the estimation of the general age of a population and to the movements of microfilariae of *Onchocerca volvulus*. Special attention was paid to the peritrophic membrane which plays an important part in limiting the number of microfilariae that survive to reach the infective stage.

Human onchocerciasis is a widespread rural problem in certain sparsely populated areas of the southern Sudan, and it is most unlikely that radical control measures against the vector will be economically practicable. Work was therefore planned to gain information on the degree of risk at different places and times and to find out what could be done in the way of partial control measures. In the section below on onchocerciasis it is pointed out that a few infective bites may do little or no harm and that therefore partial control measures may be of some value. Many aspects could only be touched on because the remoteness of the area precluded a long stay and because continued catching of flies would have exposed fly-boys to abnormal risk. Some time was spent on devising methods of work, which are described below.

Nearly all references to adult S. *damnosum* are to the females.

Methods.

Collecting.

Surveys of distribution were based mainly on collections of pupae. When only small numbers of these were found it was often useful to examine larvae as well because larvae of one species are frequently found with pupae of another.

Adult females of *S. damnosum* can easily be caught in a 2×1-in. or smaller glass tube when they are biting or about to bite. In onchocerciasis areas they were taken on local people who were in any case constantly exposed to bites, and most of the flies were captured before they had begun to suck blood. Considerable numbers of bred adults were obtained by putting unsorted pupae, still attached to grass, etc., into a tube which contained a piece of wet cotton wool covered with a disc of waxed paper and was closed with muslin (fig. 1).

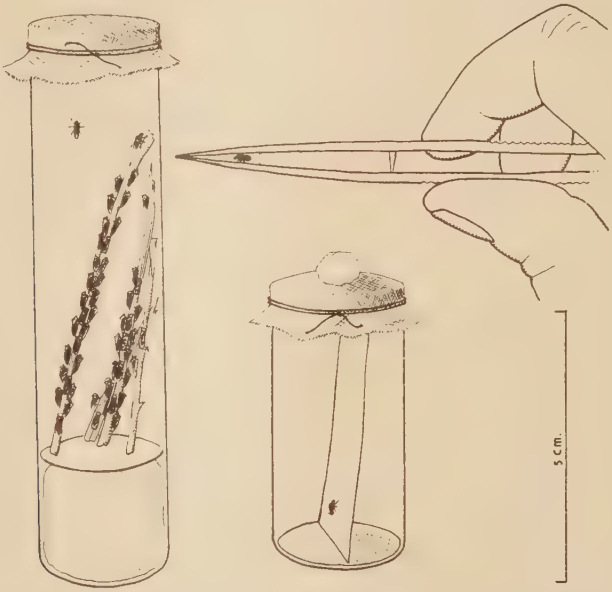


Fig. 1.—Tube for breeding flies from pupae ; tube for keeping flies alive and method of transferring a fly from a wet tube to a dry slide for dissection.

Handling in tubes.

Adults of *S. damnosum* are phototropic and can easily be transferred from one tube to another by holding the tubes so that the fly can move towards the light.

Mounting.

Pupae required for future reference were mounted in Puri's medium. Several heads of adult *S. damnosum*, from which onchocercal worms were protruding, were also mounted in this medium, and the worms, which eventually turned brown, could be clearly seen four years later.

Keeping adults alive.

It was difficult to keep Simuliids alive in captivity till Wanson and others (1945) did so by feeding them on sugar solution. In the present work fed or unfed adults were placed in 2×1-in. tubes, each of which contained a circle of filter paper and a vertical strip of it, and was closed with muslin on which was placed a piece of cotton wool soaked in sugar solution (fig. 1). The tubes were placed in an aluminium dish floating in a 4-gallon petrol tin which contained 3 gallons of water and was covered and surrounded with a folded cloth. With this rough field method it was possible to keep the flies at a humidity approaching but not reaching saturation and a temperature which varied about 1°C. in a day. Table I shows that no fly lived longer than 11 days, that many died soon after a blood meal, and that flies which had not sucked blood and were fed on sugar tended to live longer than those which had gorged. Slightly better results might have been obtained if all flies had been kept singly.

TABLE I.

Survival of *S. damnosum* kept in tubes at about 23 to 26°C. and a high humidity.

Days after capture	0	1	2	3	4	5	6	7	8	9	10	11
Caught gorged												
Given sugar	144	114	93	69	52	29	24	10	8	6	2	0
Given water	33	24	18									
Starved	26	16	4	2								
Caught ungorged												
Given sugar	49	46	38	36	35	33	25	19	10	5	2	1
Given water	8	6	4	2	2							
Starved	9	4	1									

Estimation of age.

Changes that take place in certain organs of *S. damnosum*, described in a later section, make it possible to judge whether a fly has fed on blood before, and so to ascertain readily if a population is largely composed of young flies.

Dissection.

A few drops of water were introduced by pipette into a tube containing a fly and the tube was shaken gently to wet but not stun the fly. The insect, stranded on the side of the tube, was gripped firmly but without damage, with a pair of pointed forceps (fig. 1), and transferred to a dry slide to which it adhered long enough for the wings and legs to be removed.

Flies were dissected in saline with a pointed and a flattened needle, and if minute dissection was necessary a similar, but smaller, pair of needles, made from small sharpened entomological pins in wooden handles, were used. If flies are dissected in water, instead of saline, *Onchocerca* larvae swell and cannot be measured.

In dissections to find the infection rate, the head, thorax and abdomen were mounted under ⅜-in. cover glasses and crushed. When time is short a rough search for parasites can be made by crushing the whole fly. Van den Berghe (1941a) found he could examine about 50 in an hour in this way. The mid-gut becomes so distended after a full blood meal that it cannot be removed without bursting. Therefore, when it is necessary to examine the mid-gut distended but unbroken, a partially engorged fly should be used. The oesophageal diverticulum can be removed by cutting off the dorsum of the thorax and pressing the abdomen so that the diverticulum emerges from the thorax. The abdominal organs can be exposed by severing the abdomen from the thorax, inserting a minute cutting needle under the cuticle of the venter and cutting along the whole of its length. The organs can then be scraped free from the exoskeleton.

When fresh flies are dissected to study the position of microfilariae, observations are hampered by the rapid movements of the worms, but on the other hand one can examine numerous flies in the field at various intervals after they have fed, and see if the microfilariae are active, weak or dead.

Preserved flies.

It is sometimes desirable to ascertain the infection rate in *Simulium* by examining preserved flies. Vargas (1942) did this by passing them through De Faure's (chloral-gum) medium, mounting them whole and examining them from both sides to see the worms within. In the present work flies were preserved in 70 per cent. alcohol, and for examination the legs and wings were removed and the head, thorax and abdomen mounted separately in Puri's medium and crushed. They were examined under a binocular microscope while being crushed, and later under a monocular. Microfilariae and vermiform larvae, and occasionally large sausage larvae, were seen. This method has certain advantages over dissection of fresh material. A large number of flies can be examined at leisure, and the preparations do not dry quickly and can, if necessary, be preserved for future reference without further attention. The viscosity of the medium and the fact that the worms are dead tend to prevent these from passing out of the field of the microscope or moving from one organ to another. The mildly macerating effect of the medium helps to spread the tissues. The clearing effect can be minimised by examining the specimens soon after mounting, or can be reversed by placing the preparation in a moist chamber to dilute the medium, so that the tissues regain an almost fresh appearance. Good results could probably be obtained by diluting the Puri's medium with water before mounting, and examining the flies immediately afterwards.

Fixing.

Bouin's fixative or formalin were used for flies intended for sectioning. Carnoy's was unsuitable because it hardened the blood mass in the mid-gut.

Section-cutting.

The blood in the mid-gut was liable to form a hard mass and make section-cutting difficult. This effect was minimised by avoiding or limiting the use of absolute alcohol and avoiding xylol, and by double embedding with celloidin, using soft wax and cutting thick sections. Absolute alcohol could be avoided by fixing and preserving in formalin and using methyl benzoate (Pantin, 1946) as a clearing agent before embedding in celloidin. For single embedding cedar oil was used instead of xylol. Formalin hardens chitin but for the present purpose this did not matter.

Some sections of infected flies were cut 29 microns thick and left unstained. A series of these could be examined quickly, and sometimes a complete microfilaria was seen in a single section.

Observations on O. volvulus *in* Simulium.

Infection rates.—Some published records of infection rates give little information because they include figures for newly ingested microfilariae as well as for developing larvae. The infection rate of microfilariae depends merely on the condition of the people on whom the flies happen to have been caught.

Van den Berghe (1941b) has stressed the importance of disregarding microfilariae and (1941a) suggested recording sausage-shaped larvae from 200 to 300 microns in length and long forms from 350 to 450 microns.

In the present work microfilariae were disregarded, except of course when sought for special reasons. When the collectors became practiced they generally caught the flies before they could bite, so that microfilariae were seen in few flies. When microfilariae had reached the thoracic muscles there was no difficulty about distinguishing them from small sausage larvae because flies do not feed more often than once every two or three days and this gives time for the previously ingested parasites to have taken on a distinct sausage shape. Vermiform larvae were easily distinguished by their uniform thickness and the absence of the posterior spine.

Xenodiagnosis.—Xenodiagnosis is the diagnosis of cases of disease by dissecting flies fed on suspected persons (Hinman, 1933). Ashburton (Strong & others, 1934, p. 103) suggested that it might be used for detecting microfilariae of *Wuchereria bancrofti* when very few were present, and Goldman (1944) referred to its use in the study of onchocerciasis.

By means of xenodiagnosis many people can be rapidly examined after little or no persuasion, and, if necessary, several examinations can be made of one person. Wild-caught flies were used but there was little chance of their containing microfilariae already because, as mentioned above, flies usually feed only once in two or three days and rarely if ever make interrupted meals. In any case it is easy to dispel any doubt by examining several flies caught on one person.

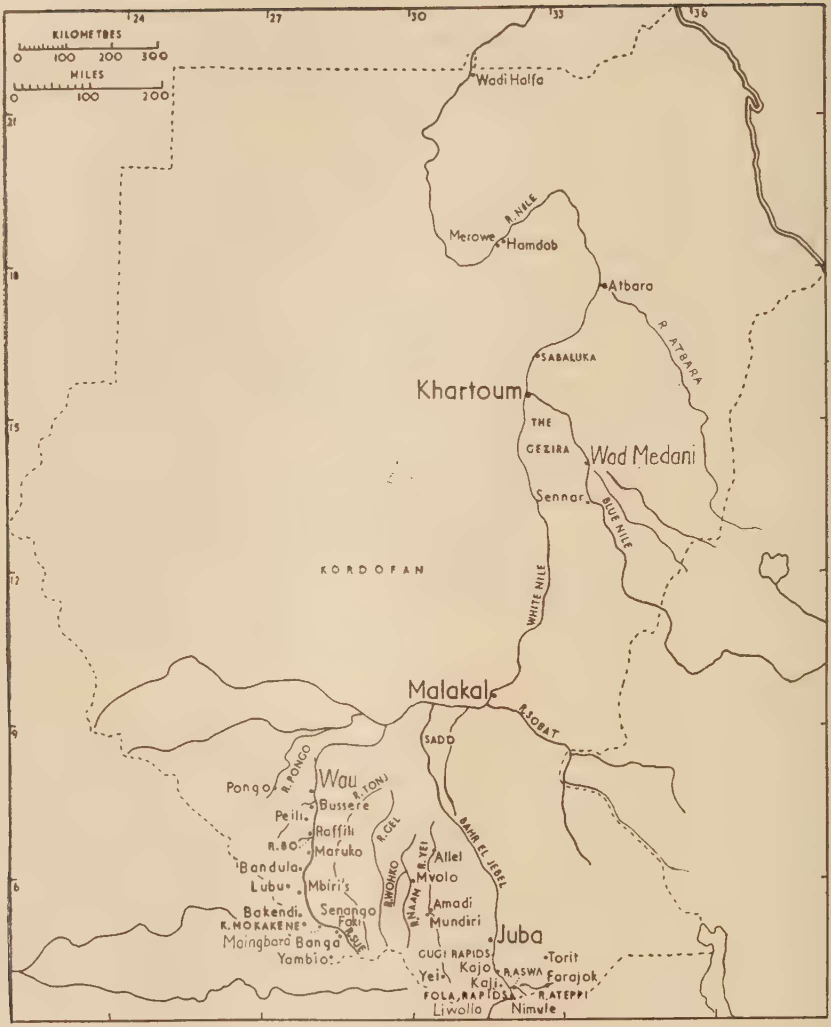
Xenodiagnosis was used for detecting heavily infected persons required for experimental infection of flies, for ascertaining the general human infection rate in certain places, and for detecting onchocerciasis in areas like Senango Faki where it had not been known before. For this latter purpose an area was regarded as infected if developing larvae of *O. volvulus* were found and if microfilariae were seen in flies which had bitten people.

Life-history of O. volvulus.—Information was obtained about the movements of the parasites in the fly.

The Country and Climate.

The Sudan (fig. 2) comprises the greater part of the basin of the River Nile. In general the country slopes gently from south to north but there are a few high mountains and many isolated rocky hills. The Nile, flowing in from Uganda, passes through a series of rapids as far as Juba and then through the swampy Sadd region to a nearly flat reach from Malakal to the Sabaluka Gorge. Thence it flows through a series of cataracts and calm reaches to Egypt. From the south-west the Nile receives tributaries which flow through the main onchocerciasis region, and further north it is joined by the Sobat, Blue Nile and Atbara rivers. Most of the south-western tributaries except the Sue cease to flow a few weeks after the dry season begins, apart from a few trickles of water at isolated points. In the south the climate is moderate and most of the country is covered with bush. The far north is desert.

Mvolo was chosen for most observations because *S. damnosum* is abundant and cases of onchocerciasis numerous, and because this place is more accessible by road than other infected areas. Mvolo is situated in grass woodland country on the River Naam where it flows over a series of rapids shortly before entering the grass plains in the north. These rapids are formed where the river crosses a chain of very large rocks which were mentioned by Schweinfurth (1873) (pp. 180–182 of third edition) and seen by Petherick in 1863. The rocks in the rivers are bare of vegetation (Lewis, 1948, Pl. 1), but in the neighbouring River Wohko Schweinfurth found a species of PODOSTEMACEAE. The Naam runs from about May to December. The survival of *Simulium* between January and April is discussed later. In 1942 the estimated mean monthly flow of the Naam in millions of cubic metres a day, from May to November, was 0·7, 2·7, 2·9, 4·7, 2·9, 0·7, 0 (Hurst & Black, 1945). Emin (Schweinfurth, 1888, pp. 326, 395) observed great numbers of fish, predacious species following cichlids, migrating downstream at the end of October, and heard of an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Wadi Halfa
R. NILE
Merowe
Hamdob
Atbara
R. ATBARA
SABALUKA
Khartoum
THE GEZIRA
Wad Medani
Sennar
BLUE NILE
KORDOFAN
WHITE NILE
Malakal
R. SOBAT
SADD
Pongo
R. PONGO
Wau
R. TONJ
Bussere
Peili
Raffili
R. BO
Maruko
Bandula
Lubu
Mbiri's
Bakendi
K. MOKAKENE
Senango
Faki
R. SUE
Maingbara
Banga
Yambio
R. GEL
R. WOHKO
R. NAAM
R. YEI
Allel
Mvolo
Amadi
Mundiri
BAHR EL JEBEL
Juba
GUGI RAPIDS
Torit
Yei
Kajo
Kaji
R. ASWA
Farajok
FOLA RAPIDS
R. ATEPPI
Liwollo
Nimule

Fig. 2.—Showing places mentioned in the text.

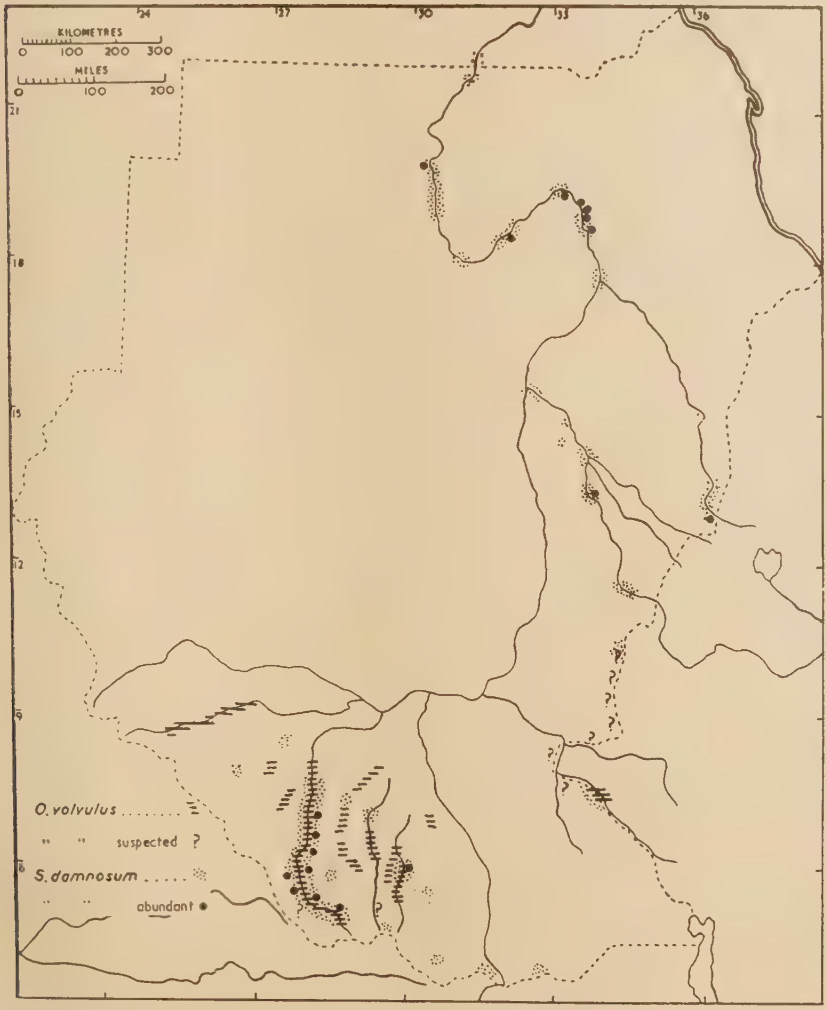
upstream migration in June. Fishing attracts many people to Mvolo, chiefly in November and December.

The mean annual rainfall, 1,129 mm., is almost confined to the period from May to October. Temperatures are recorded at Wau which has a rainfall of 1,104 mm. and a rather similar climate. The average maximum temperature there is 33·0°C. in the rains and 36·5°C. in the dry season, and the average relative humidity at 14.00 hours is 51 and 25 per cent. respectively. In the dry season the dryness of the soil and the general lack of herbage tends to make conditions even less suitable for adults of *Simulium*. There is a thin fringe of dense bush along the river. Inland the country is covered with grass and light bush, and in the dry season the ground is waterless, most of the foliage disappears and the grass dries up or is burnt.

Mvolo is 700 metres from the river and consists of a small settlement of police and other persons connected with a chief's court-house. The small school has been abandoned owing to onchocerciasis. A further 1·5 km. from the river is a village and at various points on the Juba-Wau road are situated camps for road repair gangs. At Raffili and Wad Medani, where other observations were made, the rainfall is 1,161 and 385 mm. respectively.

The Distribution of *S. damnosum.*

The known distribution of this species and the places where it is abundant are shown in fig. 3. Detailed records are given by Lewis (1952). *S. damnosum* is the most widely distributed species in the country and occurs on most rivers and large streams and on some small streams, except in the region of the great swamps and very arid areas and in places where water runs slowly or is heavily laden with silt.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27
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KILOMETRES
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MILES
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18
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6
O. volvulus .... ≡
" " suspected ?
S. damnosum ..... ⁘
" " abundant ●

Fig. 3.—Showing approximately the known distribution in the Sudan of human onchocerciasis (after Bryant, 1935, and others) and of *S. damnosum.*

In some places there are "*Simulium* years" in which *S. damnosum* is more abundant than usual (Lewis, 1948).

Places with many adults.

The places where *S. damnosum* is numerous enough to be a pest and to maintain transmission of onchocerciasis are limited, and are all situated on rivers, usually near rapids. In many places, like Khartoum, adults are found only in small numbers. In others, such as Liwollo and Yei, pupae occur but adults are unknown, a situation comparable to one described by Buckley (1949) in Kenya with regard to *S. neavei* Roubaud.

Unexpected absence or scarcity of S. damnosum.

The presence or absence of *S. damnosum* can usually be predicted from a knowledge of the local type of river. If no pupae are found a temporary rise of water level may be responsible, but there are a few areas where *S. damnosum* has not been found although conditions appear to be suitable for it.

The Nimule–Juba reach of the Nile.

There are several rapids on this part of the Nile, which have been described by Stigand (1923). No *S. damnosum* were found at the Gugi Rapids (Lewis, 1948). In October 1949 the writer visited the Fola Rapids to obtain *S. damnosum* for dissection. None could be found; fishermen appeared to know nothing of them, and none has ever been reported from the neighbouring port of Nimule. The only *Simulium* seen were two pupae of *S. adersi* Pomeroy in a backwater. There are no villages near the rapids but game is plentiful and it seems unlikely that lack of food for the flies can account for their remarkable absence or scarcity. The reason can scarcely be that they have died out and failed to regain the area because adults have been found at Kajo Kaji in the hills west of the river and pupae at Farajok on a tributary, the Ateppi. At the Fola Rapids, the Nile rushes down a narrow channel and at the point visited, at the lower end of this channel, the water surges up and down about half a metre twice a minute so that the rocks at the edge of the river resemble the inter-tidal zone of the sea shore. They are slippery with algae and support scarcely any grass or shrubs which might trail in the water. The river, fed by the great lakes, varies little in level so there is no season when the water runs in many small channels. It seems probable that since the river is confined to a narrow channel, the current is everywhere too fast for larvae of *S. damnosum*, faster than the 3·5 to 4·5 km. per hour considered suitable by Wanson and Henrard (1945), and that the surging water prevents the adults from laying eggs.

The River Aswa.

On the River Aswa, where it is crossed by the Juba–Nimule road, there are rapids which appear to be suitable for *S. damnosum*. In October 1949 numerous pupae of *S. arnoldi* Gibbins were found but none of other species. *S. arnoldi* is closely allied to *S. bovis* De Meillon which often breeds in company with *S. damnosum*. The Aswa dries up every year at this point.

Mundiri.

Near Mundiri are some rapids with only a slight fall in water level but with a strong current. *S. damnosum* occurs there but has not been found to be numerous, although on one occasion many were caught at Amadi not far away.

Torit.

The small rapids near Torit were found to contain no Simuliids but are said to dry up occasionally.

Changes in the Fly and some of its Organs with Particular Reference to Estimation of Age and to Movements of Microfilariae.

The anatomy of *S. damnosum* closely resembles that of *S. ornatum* (which was described by Smart, 1935), with the exception of the accessory glands and spermatheca. The present observations were made chiefly on the changes in the appearance of certain organs and on the structure and development of the peritrophic membrane. The effect of this structure on microfilariae is described in a later section.

The estimation of age.

The principal method of estimating the age of an Anopheline mosquito (Christophers & others, 1939 ; Russell & others, 1946) is to examine the state of development of the ovaries and to decide if the insect is passing through its first or a subsequent gonotrophic cycle, by a minute examination of the oviduct or, in a few cases, by finding old eggs remaining in the body after a previous oviposition.

When *S. damnosum* has passed through one gonotrophic cycle, which lasts two or three days, one can usually tell that it has done so from the opacity of the halteres, the reduction of the fat body, or the presence of an old peritrophic membrane. The condition of the halteres and fat body can be rapidly ascertained, the former by external examination and the latter by simple dissection or merely by crushing the insect. Changes which occur in these and other organs are described below. Some stages of them occur during the gonotrophic cycle and are not seen in freshly caught specimens because the flies do not bite during the period of egg development.

Time did not suffice to verify that the observed changes took place in every individual but there is no doubt that a population of young flies can be rapidly recognised in the course of dissection.

As in Anophelines, these estimates of age are dependent on frequency of feeding and on temperature, and at best can only be approximate. They can be useful nevertheless. For example, on several occasions flies from endemic onchocerciasis areas were dissected but very few or no *O. volvulus* were found. In each instance the appearance of the halteres showed that almost all the flies were young.

In an area with a high *Onchocerca* infection rate in the fly the condition of the worms often gives some information on age of flies and also enables one to check the value of the above-mentioned methods of estimating age. According to the known rate of development of the parasite the approximate minimum ages indicated by the presence of different stages of the parasite are : small sausage larvae, two days ; large sausage larvae, four or five days ; vermiform larvae, six or seven days ; vermiform larvae and small sausage larvae (double infection), eight to ten days; vermiform larvae and large sausage larvae, ten to thirteen days.

External appearance.

A recently emerged fly has whitish halteres and a thin abdomen. After it has fed on blood its abdomen is greatly distended and red in side view, and the halteres soon become yellow when seen by daylight. The oesophageal diverticulum can often be seen, through the antero-ventral wall of the abdomen, as a translucent, irregularly contracting body. Two or three days after a blood meal the eggs cause the abdomen to appear grey in side view.

The Halteres.

When observed by transmitted light during dissection, the haltere knobs of a newly emerged fly are translucent and the large cells which they contain are clearly seen. When newly emerged males or females, or young flies caught while biting, are kept for a day or two, supplied with raisins, a deposit appears in the knob which renders it more or less opaque, in contrast to the clear shaft, and obscures the cell structure. Wigglesworth (1949) found that in *Drosophila* glycogen, which is present only as a trace in the haltere of the newly emerged fly, is deposited in this organ, gradually increasing till four days after emergence, and disappearing in starved flies.

The deposit in *S. damnosum* was shown to be glycogen by Wigglesworth's iodine method. The halteres were cut open and the contents fixed to a microscope slide with albumen in order to allow the stain to reach them. After being stained the haltere contents were mounted in oil of cloves and retained a reddish brown colour which was not seen in halteres which had been treated with diastase.

In *S. damnosum* the haltere can become clear again in flies kept for several days, and one fly, which contained some old eggs, showing that it had fed previously, had clear haltere knobs. It appears, however, from numerous observations during dissection, that the opacity of the haltere knob usually serves to differentiate old from newly emerged flies.

Wigglesworth pointed out that glycogen was the chief reserve substance of the fly, and that glycogen in the knob was of little significance for the supply of energy. He suggested that it might have a mechanical function by increasing the mass of the knob and slightly improving its efficiency as a gyroscopic sense organ. Pringle (1948) remarks that most lower Diptera have long thin abdomens, which must increase their inherent stability in flight. He points out that inherent stability hinders rapid turning, and that this may account for the gradual reduction in length of the abdomen as haltere efficiency increases in the higher flies. Dr. Pringle has examined the halteres of *S. damnosum* and found that both scalpal plates of campaniform sensilla and the basal plate were well developed. There was a clear "unbestimmte papille" (Pflugstaedt) near the basal plate but neither of the groups of "Hicks sensilla" could be seen. The organ was well developed for a Nematoceran. The diagonal orientation of sensilla (considered to be necessary for the gyroscopic function) on the basal plate showed a remarkable similarity with a Muscid or a Syrphid. The "Hicks sensilla" were few in number but this may have little significance since no particular rôle has been assigned to them. These findings by Dr. Pringle are particularly interesting in view of the similarity in general shape between Simuliids and higher Diptera.

The oesophagus and its diverticulum.

Behind the thickly chitinised pharynx, the thin-walled oesophagus extends for a short distance and is slightly expanded in front of the proventriculus. At this point the duct of the diverticulum passes backward to that organ which, in a newly-emerged fly, is a small thin-walled crumpled sac in the thorax. In older flies it is full of fluid and lies in the abdomen, beneath the mid-gut, showing occasional peristaltic contractions.

In caught flies the diverticulum contains no air bubbles but is distended with a clear colourless refractive rather viscous fluid. Samples of this fluid from 12 flies from Wad Medani and Sennar were tested for sugar by means of paper chromatography by Mr. H. D. Fowler. He detected glucose and fructose in each sample, and sucrose in several. The glucose was present in considerable quantities and it is likely that the fluid is derived from the nectar of flowers.

If flies are caught, with the mid-gut either engorged or empty, and allowed to feed on sugar solution, the diverticulum becomes distended, often so much so after a few days that it occupies most of the abdomen. In flies fed on raisins the diverticulum contains brown material and crystals.

It seems probable that the diverticulum has a similar function to that of mosquitos, in which sweet juices or exudates from fruit go first into the crop and are then conveyed at intervals to the mid-gut (Wigglesworth, 1939).

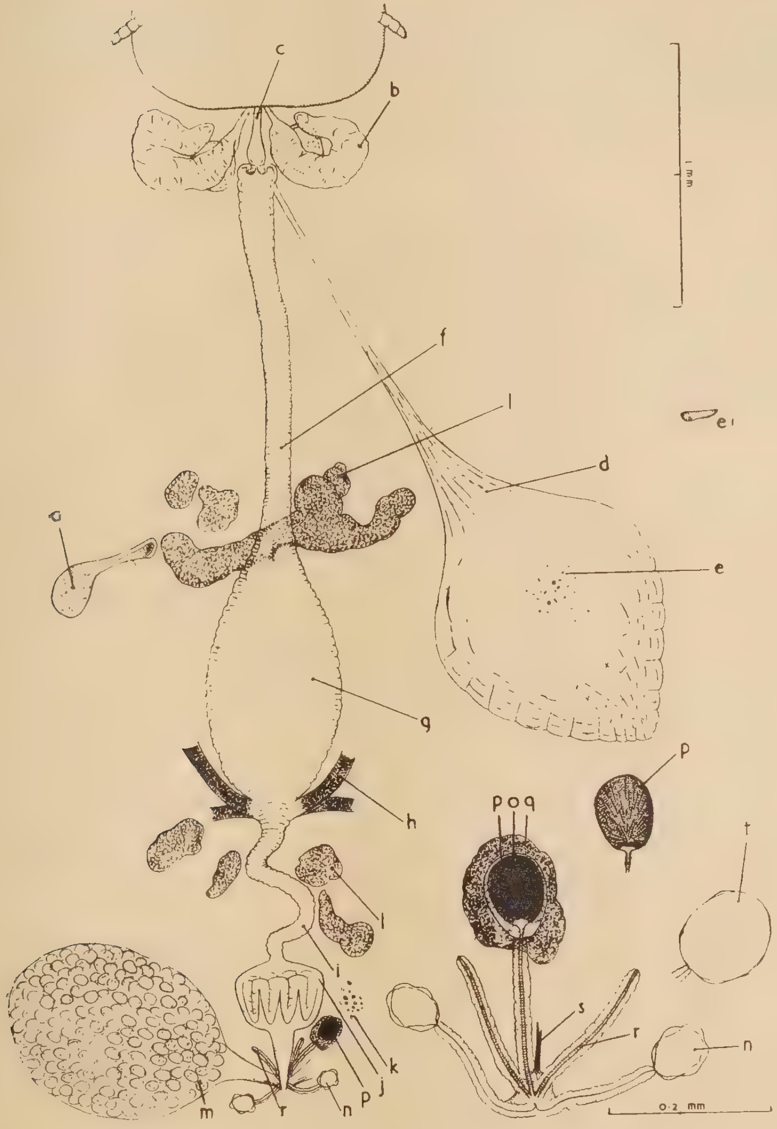
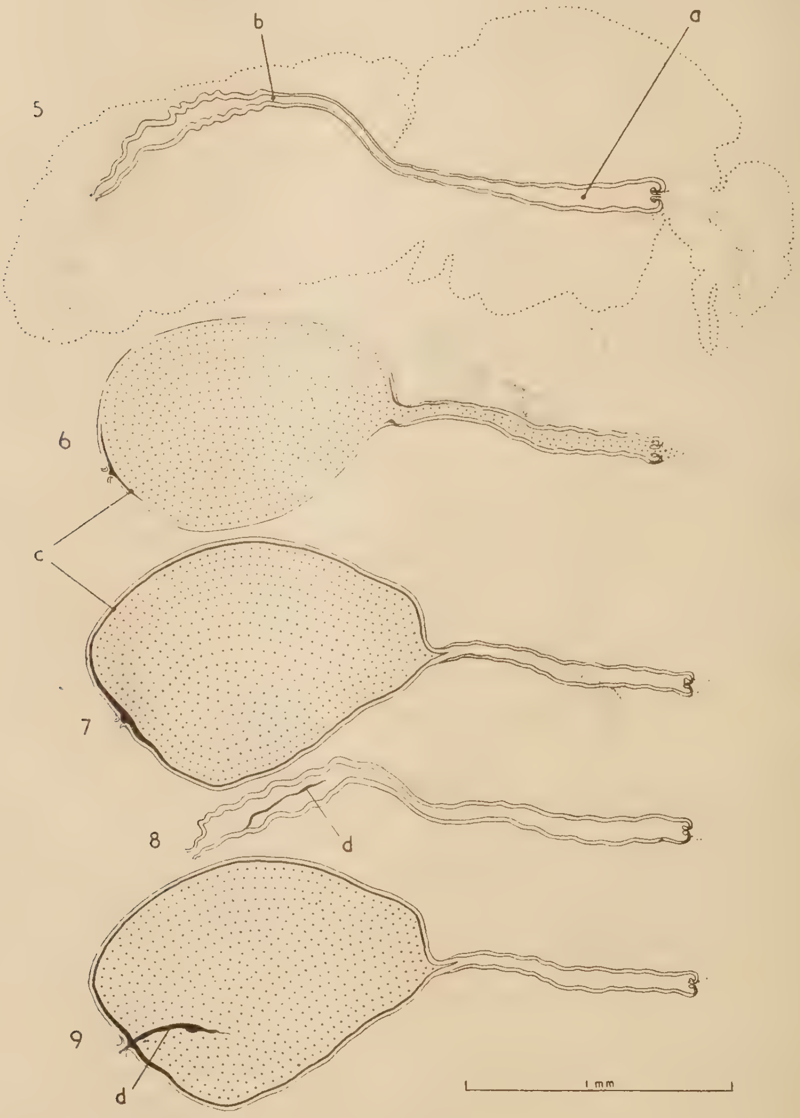


Fig. 4.—Showing certain organs of a young female of *S. damnosum* as seen during dissection : (*a*) haltere ; (*b*) labial glands ; (*c*) oesophagus ; (*d*) oesophageal diverticulum ; (*e*) grit ; (e^1) unusually large particle of grit ; (*f*) tubular part of mid-gut ; (*g*) expanding part mid-gut (the peritrophic membrane not yet formed) ; (*h*) Malpighian tubes ; (*i*) hind-gut ; (*j*) rectum ; (*k*) brown granules ; (*l*) part of fat body ; (*m*) ovary ; (*n*) accessory gland ; (*o*, *p* and *q*) epithelium, chitinous part and brown covering of spermatheca ; (*r*) duct of vestigial spermatheca ; (*s*) chitinous fork ; (*t*) accessory gland of gravid female.

In many flies the diverticulum contains a variable quantity of gritty particles of various shapes, colours and sizes. One exceptionally large one (fig. 4e^1), green in colour, was 138 microns long and 39 thick. A few particles appeared from their shape to be of organic origin, but may have been mingled with the grit when this was ingested.



Figs. 5–9.—Semi-diagrammatic sections of the mid-gut of *S. damnosum* : (5) before the first blood meal ; (6) during the first blood meal ; (7) immediately after the first blood meal ; (8) before a second meal ; (9) after a second meal. (*a* and *b*) tubular and expanding parts of mid-gut ; (*c* and *d*) new and old peritrophic membranes.

According to Patton and Evans (1929, p. 152) blood ingested by *Simulium* passes straight into the diverticulum and is almost immediately propelled into the mid-gut. Vargas (1942) referred to blood entering the diverticulum of *S. ochraceum* Walker. Blacklock (1926 a) never found blood in the diverticulum of *S. damnosum*. Neither has the present writer while examining hundreds of flies dissected after a blood meal and several flies killed during a blood meal and dissected immediately afterwards or sectioned. It is virtually certain that blood never enters the diverticulum of this species.

The mid-gut and peritrophic membrane.

The mid-gut consists of a thoracic tubular part and an abdominal part which receives the blood meal and becomes greatly distended in doing so. The peritrophic membrane (Lewis, 1950) develops in the expanding part, after a blood meal, but not after a meal of sugar solution. The normal changes which occur in the mid-gut are described below as they are seen mainly in gorged flies kept at between 23° and 25°C. and examined at intervals. Diagrams of the mid-gut are shown in figs. 5 to 9 and sections in figs. 10 to 23. Sometimes different changes, which are described later, took place in flies which had ingested large numbers of microfilariae.

Newly-emerged flies.

The expanding part of the mid-gut is slightly coloured by a brownish fluid. In sections the epithelium and its striated border can be seen without trace of a peritrophic membrane (figs. 11–13).

Flies killed during a blood meal.

Sections show blood in both tubular and expanding parts. In the expanding part, the wall of which is stretched and thin, blood corpuscles are in contact with the striated border since the peritrophic membrane has not yet formed (figs. 15 and 16). Strips or small masses of material which appear to be the first traces of it (fig. 15 *i*) are sometimes seen between the gut wall and the blood in the antero-ventral region and near the pyloric sphincter.

In flies which have sucked blood previously the remains of an old membrane may be seen, sometimes gripped by the pyloric sphincter and projecting into the hind-intestine (figs. 9, 22 and 23).

In some sections the ingested blood is seen to contain particles of other substances.

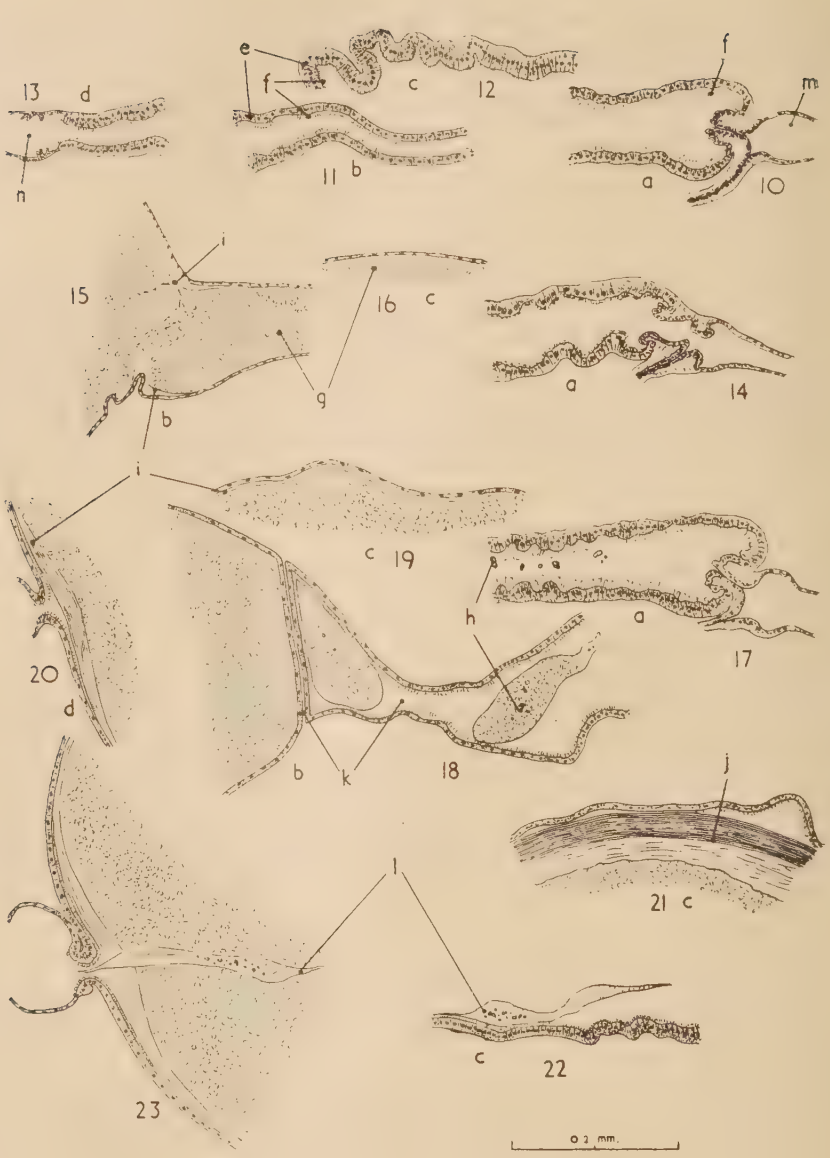
Flies killed immediately after a blood meal.

All the blood is now in the expanding part of the mid-gut except for a minute quantity in the posterior end of the tubular part (figs. 7 and 18).

From half a minute to one hour after a blood meal.

The tubular part of the mid-gut, although now almost devoid of blood, often contains some gritty particles (figs. 17 and 18) similar to those found in the oesophageal diverticulum. It is thought that this organ, under pressure from the expanding mid-gut, may disgorge some of its contents into the oesophagus from which they pass into the mid-gut.

When flies are dissected half a minute after the end of a blood meal, the blood is found to be completely enclosed by a very delicate membrane (fig. 7). This is transparent and practically invisible so that it can usually be detected only by the fact that it restrains the movement of the blood corpuscles. When microfilariae are present they also reveal the membrane by pushing against it and sometimes raising it into small folds. The membrane is still difficult to see after ten minutes, but half an hour later appears as a well-defined outline to the blood mass.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0·2 mm.

Figs. 10–23.—Sections of the mid-gut showing changes during and after a blood meal: (10–13) before a meal; (14–16) during a meal; (17–21) after a meal; (22 and 23) before and during a second meal. (*a*) tubular part of mid-gut; (*b*) junction of tubular and expanding parts; (*c*) centre of expanding part; (*d*) posterior end of expanding part; (*e*) epithelium; (*f*) striated border; (*g*) blood; (*h*) ingested particles other than blood; (*i*) peritrophic membrane; (*j*) thick membrane in a fly which has had a small meal and been killed 90 minutes later; (*k*) normal distortion due to twisting of gut; (*l*) old membrane; (*m* and *n*) oesophagus and hind-gut.

The membrane has a minute anterior pointed process and a posterior blunt knob. The process projects slightly into the tubular part of the mid-gut and, like it, often contains a few gritty particles. The posterior knob lies against the pyloric sphincter.

If the mid-gut is cut the blood mass within the membrane can be removed without breaking the latter. The mass is slightly elongated and also flattened dorso-ventrally, probably by pressure from the oesophageal diverticulum beneath. One such blood mass, of about 1·1 cu. mm., which was measured after removal from the fly and ten minutes after a blood meal, was 1·43 mm. long, 1·27 mm. wide and 1·22 mm. deep. Another was 1·56 mm. long and 1·19 mm. wide.

From 1 to 24 hours after a blood meal.

Sections of flies killed about an hour after a blood meal show the membrane between the blood mass and the striated border of the mid gut epithelium. In some places, particularly near the posterior knob, it is clearly laminated and is thought to consist of successive layers of material secreted rapidly by the mid-gut epithelium. Up to about 30 laminae can be seen near the knob. The laminated nature of the membrane is particularly well seen when, occasionally, some of the laminae become separated from each other during the cutting of sections.

In one fly, killed 90 minutes after a small blood meal and sectioned, the outer half of the membrane, near the epithelium, showed about 15 distinct laminae, and the inner half was not clearly laminated and had an irregular inner surface (fig. 21). The membrane was very thick, 63 microns in places. It is probable that the mid-gut epithelium secretes as much membrane material after a small meal as after a large one and that the blood mass after a small meal therefore becomes enclosed by a thicker membrane.

When a sample of the membrane was examined by Wigglesworth (Lewis, 1950) it gave a positive reaction to the chitosan test (Wigglesworth, 1939) for chitin. The membrane is tough, often remaining intact when the surrounding gut wall bursts during dissection. It is inelastic and so does not contract when it is broken and the contained blood is squeezed out. The membrane gradually turns brown but remains unbroken for a long time. In two flies dissected six and 20 hours after a blood meal the membrane was yellow anteriorly and brown posteriorly. In three flies dissected six hours after a meal, in two after 16 hours, in two after 20 hours, and in one after 23 hours the membrane was still unbroken. In one seen after 20 hours the membrane had broken, possibly during dissection. The membranes of two flies were compressed with a cover glass six hours after a blood meal and burst at or near the posterior knob. Two membranes which were similarly treated after 16 hours burst at each end.

In replete flies the peritrophic space (between the membrane and the mid-gut wall) is very small, but, if flies are dissected in normal saline and water is added the space immediately increases, presumably by inflow of water through the gut wall owing to osmotic pressure.

From 24 to 72 hours after a blood meal.

During this period the membrane breaks and most of the blood mass disappears. In one fly dissected 43 hours after a meal the mid-gut contained brown remnants of the blood and membrane. In three examined after 48 hours the membrane of one was broken but otherwise complete, and those of the other two appeared to be still unbroken. Sections of a fly killed long after a meal showed a brown fragment of membrane adhering to the gut wall (fig. 22). Sometimes the anterior tip of the old membrane is seen to contain particles (fig. 23) which probably originated in the oesophageal diverticulum.

The membrane in some heavily infected flies.

In some flies which have ingested more than 100 microfilariae the blood mass is not confined to the mid-gut but blood and microfilariae are seen in the hind-gut shortly after a blood meal. It is thought that the massed struggling microfilariae force open the pyloric valve and prevent the normal formation of the peritrophic membrane which therefore does not prevent the passage of blood backward.

It was shown that this condition was natural and not due to any rupture during dissection. Some of the above-mentioned flies were carefully dissected from behind so that no pressure was put on the mid-gut and in two flies the condition was observed in sections. Furthermore, the blood was seen in the hind-gut of one fly through the body wall before dissection, and several others passed faecal droplets of blood and microfilariae shortly after feeding, showing that blood had reached the rectum.

Summary of the apparent principal changes.

The sequence of events during and after a blood meal appears to be as follows.

A relatively large volume of blood enters the mid-gut and is confined to the expanding part of it. Some material enters the tubular part from the oesophageal diverticulum. During the meal the epithelium of the expanding part begins to secrete a peritrophic membrane which completely encloses the ingested blood within half a minute or less of the end of the meal. The membrane is essentially a tube, closed at each end by the contracted parts of the gut at points which later become potential breaking points. The anterior one is a delicately tapering point and the posterior one a thick blunt knob formed against the pyloric sphincter. The membrane is chitinous, tough and inelastic, and is laid down in a series of laminae which probably continue to be added for a short time. The membrane usually remains complete for over 24 hours and part of it is seen when the blood has disappeared.

In flies very heavily infected with microfilariae the normal process of enclosure of the blood by the membrane fails to occur and some blood passes rapidly to the hind-gut. Probably the parasites force open the pyloric valve and so prevent the completion of the membrane.

Comparison of the membrane with those of other insects.

The peritrophic membrane differs from the two main types found in insects, and described by Wigglesworth (1939), in its formation from the posterior part of the mid-gut, in its closely laminated structure, and in forming a complete envelope round the food. It has no connection with the cardia which secretes membranes of the narrow tubular type.

The membrane in other Nematocera.

A peritrophic membrane is found in *S. griseicolle* Becker (Lewis, 1950) and may occur in other species without having been noticed because it does not exist in ungorged flies. None was seen by Smart (1935) in *S. ornatum* Mg. but he examined unfed specimens. Vargas (1942) did not mention a peritrophic membrane in the South American *S. ochraceum* Wlk., and his reference to blood in the fore part of the mid-gut and the oesophageal diverticulum suggests that the digestion process in that species may differ from that of *S. damnosum.*

Peritrophic membranes have been found in *Anopheles* and *Phlebotomus* by Yaguzhinskaya and Dolmatova respectively (Lewis, 1950). It is not known if these are like those of *Simulium* but the general shape must be different because the mid-gut of *Simulium* swells to an almost spherical instead of an oblong shape.

The function of the peritrophic membrane.

The peritrophic membrane of insects was generally thought to protect the mid-gut wall from abrasion by hard fragments in the food (Wigglesworth, 1939), and this belief was supported by the apparent absence of the membrane from many blood-sucking insects such as adult Tabanids, mosquitos, fleas, lice and many others in which no mechanical protection appeared to be necessary, although *Glossina* was known to possess a membrane. Now, however, a peritrophic membrane has been found in Tabanids (Olfus'ev, quoted by Yaguzhinskaya), *Anopheles*, *Phlebotomus* and *Simulium*. Observations recorded in the present paper show that in *S. damnosum* the membrane normally protects flies which have ingested microfilariae of *O. volvulus* by reducing the degree of infection. The membrane also obviates the need for prolonged muscular contraction at each end of the expanding part of the mid-gut to keep the blood mass in position during digestion.

The Malpighian tubes.

These vary in appearance from being transparent to nearly opaque, but few precise observations were made.

The hind-gut.

In newly emerged flies the hind-gut often contains opaque pink material.

Brown granules.

In newly emerged flies numerous brown granules, possibly derived from the larval fat body, are to be seen in the body cavity, particularly near the tip of the abdomen. They are much less numerous in older flies.

The main fat body.

The main part of the fat body comprises two groups of colourless masses, one lying in front of and the other behind the expanding part of the mid-gut. There is a large quantity of this fat body in newly emerged flies, and as Rubtzov (1940) observed, it diminishes during egg development.

The ovaries.

The eggs only develop after the insect has fed on blood. In a young female caught in the act of biting the ovum in a follicle is clearly distinguished from the nurse cells by a number of transparent granules. Soon after the insect has fed the follicle becomes larger and the ovum opaque owing to the appearance of numerous yolk granules as in the third stage of development in Anophelines.

The period of development varies from about two to three days. Some flies kept at 25°C. have, when handled, laid eggs 48 hours after sucking blood. After oviposition some old eggs often remain behind, sometimes two or three as in mosquitos, and sometimes up to 20 or more.

The accessory glands.

In young ungorged females the two accessory glands are much smaller than the spermatheca and have thick uneven walls. After a blood meal the glands swell and their walls become thin and smooth (fig. 4 *t*). The contents are a clear fluid with a few small colourless particles. Before oviposition each gland is about as big as the chitinous part of the spermatheca, but immediately afterwards, with their contents discharged, they have returned to their original appearance. Two narrow ducts lead from the glands to the genital opening.

The spermatheca.

Three other ducts, with transverse chitinous thickenings (fig. 4) lead to the genital opening, one from the spermatheca and two from blind ends which, I understand from Dr. B. Jobling, are vestigial spermathecae.

The internal surface of the spermatheca is a strong dark chitinous capsule (fig. 4 *p*) with numerous long thin spicules directed inwards towards a point near the opening into the duct. Round the capsule is the epithelium to which is loosely attached a mass of brown tissue, apparently fat body, containing numerous brown particles, which show marked brownian movement. According to Rubtzov (1940) this tissue, in another species, consists of unicellular glands with brownish contents.

Before fertilisation or after oviposition the spicules are easily seen, but at other times they are partly obscured by spermatozoa. In the course of time the brown tissue round the spermatheca becomes reduced and divided into partly separate masses revealing the underlying epithelium more clearly. The brown tissue is apt to be dispersed by pressure from a cover glass.

Other structures.

Some other parts of the insect doubtless show changes with age but have not been studied because some of the above-mentioned organs afford useful information. The cuticle is of course rather soft at the time of emergence and hardens later. The wings may, as in tsetse flies, become frayed, and probably some of the thoracic and abdominal scales are lost. The salivary (labial) glands show little or no change in appearance, and the oviducts have not been examined for change in diameter.

Other Observations on *S. damnosum.*

Seasonal changes in numbers.

The main breeding season in the southern and northern Sudan are at opposite times of year. In the south the rainy season (May to October) is the principal breeding period and in the dry season breeding becomes gradually confined to a few isolated points. In the north *S. damnosum* has not been found during the rains, when the rivers are very turbid, but in the dry season breeds till about April when the hot dry conditions are unfavourable to the adults.

At Raffili, adults of *S. damnosum* were found in every month of the year but were reported to be scarce in March and very scarce in April.

TABLE II.

Pupae collected at Mvolo.

Period	Species of *Simulium* :*					Total
	adersi	*bovis*	*damnosum*	*griseicolle*	*mcmahoni*	
1941						
Dec. 19 ...	—	—	253	—	—	253
1948						
May 25–31 ...	85	3	2	1	—	91
June 1–7 ...	313	82	12	71	—	478
,, 8–14 ...	159	87	15	49	—	310
,, 15–21 ...	—	77	1	68	—	146
,, 22–30 ...	—	217	2	44	—	263
July 1–7 ...	6	1,841	25	113	—	1,985
,, 8–14 ...	—	393	13	45	—	451
,, 15–21 ...	—	13	—	—	—	13
1949						
Aug. 15–21 ...	—	60	471	4	—	535
,, 22–31 ...	—	19	187	—	1	207
Sept. 1–7 ...	—	7	—	—	—	7
Nov. 15–21 ...	—	—	9	—	—	9
	563	2,799	990	395	1	4,748

*One pupa of *S. cervicornutum* was found 2 km. upstream.

Breeding habits.

Although *S. damnosum* is often found breeding in large and small rapids, which probably constitute its main breeding places, there is little doubt that it breeds extensively in some of the calm stretches of southern rivers. It is known to breed in calm water in the north, and, in the Senango Faki area, adults are common and widespread in the country near a long reach of the Sue which is far from any known rapids.

At Mvolo pupae of *S. damnosum* could often be found in the rapids but the number obtained was surprisingly small in relation to the many thousands of adults present. In the early part of the rains (Table II) only 70 pupae were obtained between 25th May and 21st July, although several collections were usually made every ten days and 50 times as many pupae of other species were found. Most of the pupae were taken from trailing vegetation and stranded sticks, and it is thought that many *S. damnosum* breed on inaccessible rocks some distance below the surface. Some scattered pupae of this species were once found on a rock face after a rapid fall in water level. At the end of the rains pupae of *S. damnosum* were common on sticks.

Dry and wet season haunts.

Like some tsetse flies, adults of *S. damnosum* are much more widely distributed in the rains than in the dry season. During the dry season adults are often found in patches of riverain bush far from any rapids, when at the same time no flies are to be seen near breeding places in open country. During the rains in the south the fly spreads far and wide through the country although it is usually rather more prevalent near the rivers.

Observations at Mvolo.

Pupae have been found at Mvolo from May to December (Table II). When the writer arrived there on 13th May, 1949, the rains had begun but the river had ceased to flow some 14 weeks before, on 4th February, and was still a sandy channel with a few isolated pools. Several adults of *S. damnosum* were caught on 13th May. Their abdominal scales showed no signs of wear, yet no breeding place was known to exist. The river began to flow on 16th May, some weeks later than usual, and the next day *S. damnosum* became common, for no obvious reason. On 21st May a few *Simulium* larvae were found on creepers recently placed in the river for the purpose, and on 23rd May some larvae, and a pupa skin of *S. damnosum* were found on stranded sticks. On 25th May pupae of *S. adersi* and *S. bovis* were found, and on 27th May a pupa of *S. damnosum*. Adults of this species were seen daily during the rains, often biting at the rate of over 200 an hour. The numbers seen often varied from day to day and week to week. In 1949 the river ceased to flow at the Mvolo gauge on 11th December and an assistant who visited Mvolo from 29th January to 7th February, 1950, was told that the adults had disappeared a month before and was only able to obtain three flies, one on 30th January and two on 31st January, close to the rocks in the river bed.

Length of life.

There were indications that, as might be expected, most of the adults tend to live longer in the wet than the dry season. The fact that about as many flies were infected with vermiform as with sausage larvae suggested that there was little mortality in the first week or so at this season. Most flies which were examined in the dry season appeared, from the condition of their halteres and fat body, to be newly emerged.

It is conceivable, however, that a few flies can live for weeks or months in the dry season. The finding of adults at Mvolo long after the river had ceased to flow suggests that they had lived a long time. It was not possible to examine the whole district, but it seems unlikely that there was some trickle of water upstream or in the surrounding country in which *S. damnosum* could breed. Flies might perhaps live in deep damp cool clefts in the rock of the river bed. This would explain their presence near these rocks in January at Mvolo, and the sudden appearance of adults when the river began to flow.

Range of flight.

It is known that Simuliids can fly or drift on the wind for great distances. Glick (1939) trapped some in an aeroplane up to 5,000 feet. Rempel and Arnason (1947) recorded a Canadian species in numbers up to 60 miles (96 km.) from its main breeding place, and emphasised the effect of wind. In the Sudan the small species, *S. griseicolle*, can probably travel 80 km. or more (Lewis, 1948). Austen (1909) noted that *S. damnosum* could follow victims several miles from the Nile and render out-door work impossible, and Gibbins (1936) considered that it could travel 45 miles (72 km.) in Uganda. In the southern Sudan it is often seen 10 or 20 km. from a river, and one was seen at Khor Mokakene, 30 km. from the River Sue. It is difficult to obtain records of long flights in an area where there are many rivers but there seems little doubt that *S. damnosum* can cover great distances, perhaps much greater than those observed.

Material ingested by the female.

Blood.—According to Bequaert (1938) *S. damnosum* bites man, wild animals and birds. Fain (1950) discussed the food of this species and pointed out that in some parts of Africa it does not attack man. Wherever it is common in the Sudan it bites man. At Mvolo there are few domestic animals, and the blood meals of the insect are probably nearly always of human origin. Flies were seldom seen on sheep and never on fowls. Baboons are common but they showed no signs of being attacked.

Other vertebrate tissue.—Blacklock (1926a) often saw cellular debris in the gut of flies which had begun to bite but had not reached blood level. Some flies in the Sudan contained similar material.

Gibbins (1938) thought that microfilariae were ingested when the insect was enlarging the initial puncture. It is not unlikely that some tissue fluid is imbibed at this time. If so it would explain the fact that flies sometimes appear to swell but are later found to contain no blood.

Microfilariae.—Microfilariae of *O. volvulus* are often numerous enough to constitute a considerable proportion of the material ingested by the insect.

Plant food.—According to Bequaert (1934) various species of *Simulium* will visit flowers in search of nectar, and, in captivity, will suck plant juices. *S. griseicolle* is known to visit flowers.

S. damnosum has not been seen on flowers, but in January at Wad Medani minute paired pieces of plant tissue were found attached to the mouth-parts of several females. They were identified by Mr. K. W. Jones as pollinia, the club-shaped bags of pollen which occur on the stamens of certain flowering plants. They are found mainly in the Asclepiadaceae and Orchidaceae, of which the former is represented at Wad Medani (Broun & Massey, 1929). In the two species examined, *Calotropis procera* Ait. and *Kanahia laniflora* R. Br., however, the pollinia are much larger than those found on the flies. It is evident that *S. damnosum* does, sometimes at least, visit flowers, and the above-mentioned finding of sugars in the diverticulum suggests that the female normally feeds on nectar as do some mosquitos (Mattingly, 1951) and probably *Phlebotomus papatasi* (Scop.) (Kirk & Lewis, 1951).

Pollen grains (fig. 24) of at least four different kinds were seen in the mid-gut of several females from Raffili and Wad Medani and a fifth kind in the diverticulum of a female from Raffili.

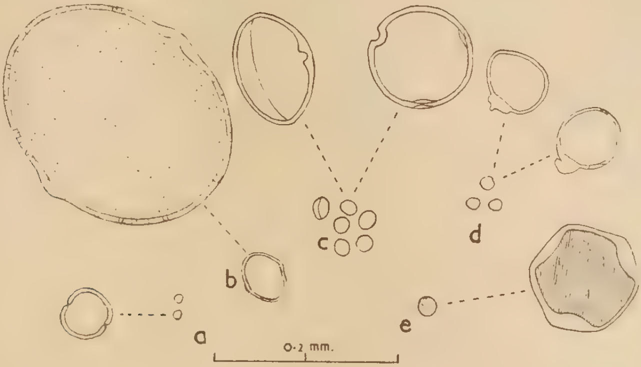


Fig. 24.—Pollen grains found in *S. damnosum* : (*a–d*) from mid-gut ; (*e*) from oesophageal diverticulum.

Grit.

The origin of the gritty material often seen in the oesophageal diverticulum is unknown. It may be that a fly drinks water from wet mud near its breeding place and so ingests mineral particles. If emerging adults are given access to wet paper on which carmine has been sprinkled, particles of the stain can be found in the diverticulum or the mid-gut.

Biting habits.

The flies nearly always bite below the knee, but occasionally attack thighs, arms or neck when the lower leg is protected by repellent. The fly moves over the skin, patting it with the forelegs as noted by Austen (1909).

Frequency of biting.—Dissections show that flies do not feed when the ovaries are developing and therefore that they do not feed more often than once every 2 or 3 days. Interrupted meals probably rarely if ever occur. If they did one would expect to find two peritrophic membranes, one within the other, and these have never been seen. Irritation is felt towards the end of a blood meal (Blacklock, 1926a) so flies are not usually brushed off when partly engorged. Van den Berghe (1941a), working in a highly infected district of the Belgian Congo, caught many flies without allowing them to bite people and rarely found any microfilariae in them. He would have found many if flies had made interrupted feeds.

Place of biting and entry into houses.—*S. damnosum* will bite almost anywhere out of doors by day, near or far from rivers, under shady trees and in large or small clearings, in entirely open country such as the Kajo Kaji plateau and the Gezira plain, on bare rocky hill tops near Bandula, and in the desert near Merowe.

The flies often bite more in the open than in bush, and a clearing 200 metres wide seems to act as a feeding ground as it might for *Glossina palpalis* (R.-D.). According to Van den Berghe (1941a) *S. damnosum* flies near the surface of the ground, but it will readily bite a man standing on boulders 3 metres high. People standing in thick grass or herbage are partially protected, perhaps because they are hidden from view.

With regard to biting indoors, Bequaert (1929) did not see *S. damnosum* in closed huts in Liberia but often found it biting people in shaded verandas and open sheds.

Bryant (1935) stated that he found it indoors at Mvolo. The present writer was informed that people who remained in ordinary dwelling huts were unmolested. He lived in an open rest-house which consisted of a mud wall and a thatch roof separate from it. There was one rather dark inner room and a veranda with a continuous gap between the thatch roof and low wall on three sides (Pl. XXIII, fig. 6). *S. damnosum* was never seen in the room, and very few bit in the veranda even when there were many outside. On one occasion a boy was stationed inside the open doorway and another, who was about equally attractive to *Simulium*, 14 metres outside the rest-house. In half an hour one fly was caught on the first boy and 76 on the second. In the court-house, a building with very high eaves and very low walls, flies bit readily.

Time of biting.—*S. damnosum* bit from before dawn till after sunset at Mvolo, and usually more during the 2 hours before sunset than at other times. They bit in light rain, and often in bright sunshine unlike those observed by Blacklock (1926a). At Hamdab in the northern Sudan, during the relatively cold winter, *S. damnosum* does not bite much till about 10 a.m.

The number of biting *Simulium* often varies from day to day. Underhill (1940) in America considered that moderate temperatures, calm air and low barometric pressure encouraged the flies to bite.

Egg laying.

This was observed in specimens which had been caught while biting, kept till they were gravid, and stimulated to lay by injury. The eggs emerge in a single ribbon and remain sticky for a short time. The shell at first stands out from the contents but soon contracts. The number of eggs laid by one of the flies was 529.

Parasites other than *Onchocerca*.

Fifteen parasites, in addition to *O. volvulus*, were found in or on *S. damnosum* (fig. 25). Only two were common, *Mermis* sp. and a Hymenopterous larva.

Protozoa.

A mass of flagellates, of a crithidial form (fig. 25 *b*) was seen in the abdomen of a few flies at Mvolo.

Protozoa which appeared to be stages of a gregarine were seen in several flies at the same place. There were large rod-shaped bodies with one or two nuclei, frequently in pairs or short chains, scanty round forms filled with circular nuclei, and very darkly staining oval bodies. In several flies, caught while biting, this parasite was found in the ovaries which had undergone partial but abnormal development (fig. 25 *c,d*). Either a few eggs had developed to full size or many had partially developed.

Microsporidia (fig. 25 *e*) were found in larvae from Bakendi. They formed large white masses, apparently the myxosporidium stage described by Strickland (1913), and probably belong to the genus *Thelohania* which, according to Smart (1944), forms such bodies in *Simulium*. Microsporidia are known to parasitise Simuliid larvae (Bequaert, 1934), and, according to Steinhaus (1946), the parasitised larvae never reach the adult stage. Wanson and Henrard (1945) found many larvae parasitised with Microsporidia in the Belgian Congo.

Ciliate Protozoa (fig. 25 *f*) were found in the abdomen of a fly at Mbiri's.

Nematode worms.

Acanthocheilonema perstans (fig. 25 *g*) was sometimes seen in the blood freshly ingested by flies at Mvolo and appeared to be common at Bandula where biting midges were prevalent.

A small worm (fig. 25 *k*) with a bent tail was seen in a larva from Lubu.

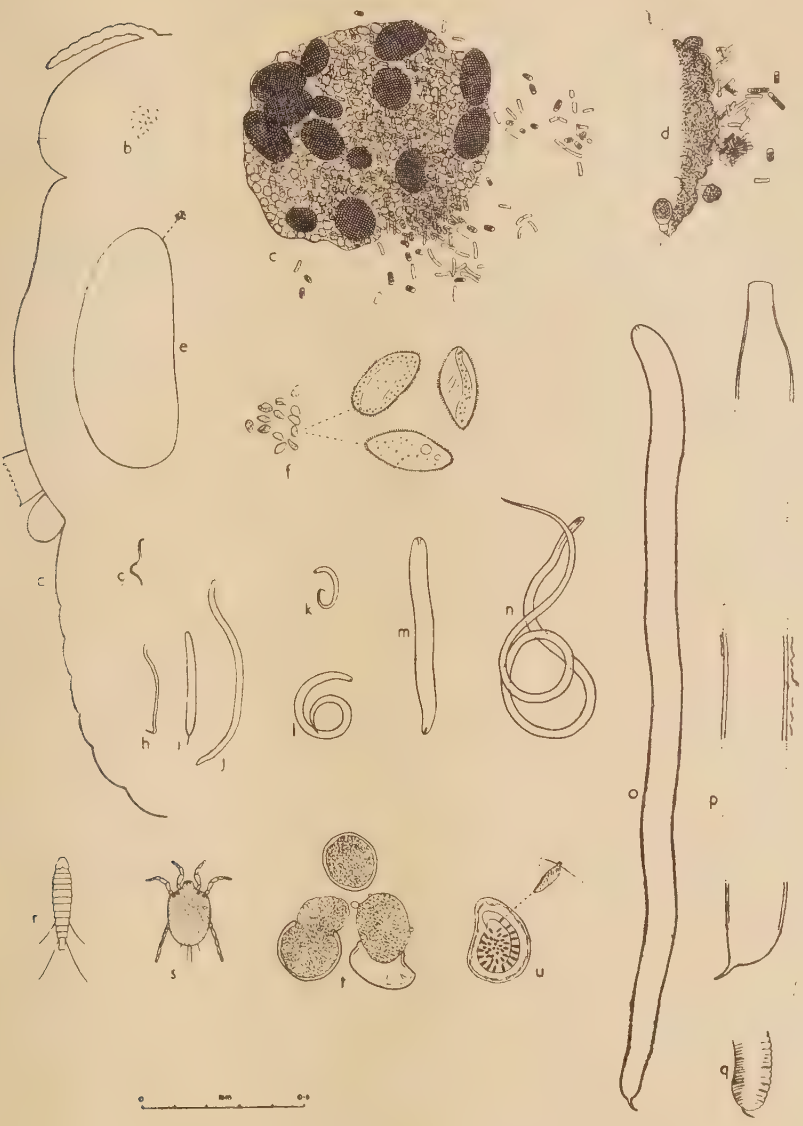


Fig 25.—Parasites of *S. damnosum* (adult flies except where otherwise indicated) seen in the Sudan, some shown in outline : (*a*) outline of an unfed fly ; (*b*) *Crithidia* ; (*c*) ovary with gregarine Protozoa bursting out of it during dissection, and only a few developed eggs ; (*d*) another parasitised ovary with all eggs partly developed ; (*e*) a small mass of Microsporidia from a larva ; (*f*) ciliate Protozoa ; (*g*) microfilariae of *Acanthocheilonema perstans* ; (*h–j*) microfilariae and sausage and vermiform larva of *O. volvulus* ; (*k–n*) unidentified nematodes (*k* from larva) ; (*o–q*) *Mermis* sp., a relatively small specimen, a broken-off tail, and parts of a large specimen from a larva ; (*r*) a planidium hymenopterous larva ; (*s*) a mite ; (*t* and *u*) unidentified parasites two of which have burst under pressure.

Two worms (fig. 25 *l*) with pointed tails were seen in the abdomens of two preserved flies from Raffili in July and October.

Two individuals of a broad slowly moving worm (fig. 25 *m*) were found, one in the head of a fly at Mvolo, and the other in the abdomen of a fly at Lubu which was also infected with *Mermis* sp.

A long narrow worm, which twisted itself rapidly in coils (fig. 25 *n*) was found in the abdomen of a fly at Mvolo, and one, probably of the same species, in the abdomen of a fly preserved at Raffili in July.

Mermis sp. (fig. 25 *o, p, q*) was found in *S. damnosum* at several places on the River Sue and its tributaries but never at Mvolo. Sixteen of 100 larvae from Bakendi were found to be infected, a few pupae from Lubu, 5 per cent. of 76 flies from Bandula, 33 per cent. of 79 from Lubu, 24 per cent. of 25 from Maruko, and 7 per cent. of 42 from Mbiri's. Of 151 flies collected at Raffili in February 1950, at least 19 per cent. were infected. In 2,226 flies preserved at the same place between October 1950 and September 1951, 0·8 per cent. were infected and the highest monthly infection rate was 3·6, in 224 flies in January. There was scarcely ever more than one *Mermis* in one *Simulium.*

In the larva the longest worm seen measured 31 mm., about five times the length of its host. The worms were sometimes coiled in the abdomen of the larva with a loop reaching forward to a point near the head, and moved very slowly. The young worms had a pale pink tinge and the older ones were green or yellow. When some larvae died in a basin of water several *Mermis* were found moving freely among the decaying bodies, and were kept alive for a day or two without difficulty in clean water. They did not burrow when placed in tubes of water and sand.

In the adult flies the worms were on the whole much shorter than those in the larvae and the longest measured 7 mm. The worms were usually coiled in the abdomen but were sometimes found in the thorax and sometimes with parts in the head, thorax and abdomen. In one instance the head, in another the tail, and in another both head and tail of a worm were in the fly's head.

Evidently many *Simulium* pupated and emerged in spite of these worms, and parasitised flies were found to have flown far from water. Forty-two of the flies from Lubu, which died within 15 hours of capture, had almost exactly the same parasite rate as the remainder, and the worms appeared to have little adverse effect on the activity of the flies.

The *Mermis* found in American *Simulium* by Strickland (1911) reached the same length as those in Sudan larvae but, unlike them, were not almost always single. Christie (1941) points out that those mermithids which hatch outside an insect and enter it by penetrating its body wall tend to be few in number and to have a propelling organ, often in the form of a horn-like appendage which persists in the fully grown larval worm. It is not known if the worms found in the present work enter the larvae through the body wall, as some species of *Mermis* do (Steinhaus, 1949).

None of these nematodes could be mistaken for *O. volvulus,* except perhaps *Acanthocheilonema perstans* and the two species shown in fig. 26 *m* and *o*. The microfilariae of *A. perstans* are smaller than those of *O. volvulus* and differently shaped. The other two species, only found, rarely, in the abdomen of the fly, can readily be distinguished by the shape of the anterior and posterior ends.

An insect larva.

A planidium larva (fig. 25 *r*), probably a species of *Perilampus* of the hymenopterous Chalcid family PERILAMPIDAE, was found in adult flies at Mvolo and Raffili and in one from Mbiri's. The larvae had two pairs of large setae on the abdomen and, exclusive of these, measured 0·26 mm. in length, being all about equal in size.

They were almost invariably in the head, usually in the region of the eye, and sometimes moved slowly.

At Mvolo and Raffili 4,108 flies were examined for *Onchocerca* and 107 of them, 2·6 per cent., were found to be infected with planidia. Altogether 126 plandia from these places were seen, 90 flies containing one each, 15 flies containing two each, and two containing three each. At Mvolo the average infection rate was 1·7 per cent. with a maximum of 10·2 in August. At Raffili, where the parasites were found in the dry and wet seasons, the average rate was 3·4 and the maximum 7·5 (in 146 flies in September). Among the 1,882 flies from Mvolo, of which 200 were infected with *Onchocerca*, nine infected and 22 uninfected flies contained planidia.

The fact that all planidia were the same size and no later stages were seen suggests that the Hymenopteran normally attacks some other host and is only an accidental parasite of *Simulium*. If this is so, however, it is surprising to find the planidia inside, instead of outside, the *Simulium*, since the planidium stage of a Chalcid is adapted to meet the conditions encountered between hatching and establishing contact with the host (Clausen, 1940). Furthermore, if the planidium were merely an accidental parasite one would expect to find very few instead of the by no means negligible rate of parasitism encountered.

Hymenopterous parasites have only once before been recorded from *Simulium* (Thompson, 1943), when Enderlein (1921) found two Braconids in pupae.

Mites.

An elongated mite was once seen on *S. damnosum* at Mvolo, and a rounded one (fig. 25 *s*) was seen several times.

Unidentified bodies.

Nearly spherical cyst-like bodies, one to three in number, were sometimes seen in larvae, pupae and adults of *S. damnosum* (fig. 25 *t*). An unidentified object containing cigar-shaped bodies was found in the abdomen of one fly from Raffili and one from Mvolo (fig. 25 *u*).

S. damnosum and Onchocerciasis.

Human onchocerciasis in the Sudan has been studied by Bloss (1949 ; Sudan Medical Service, 1950, p. 42), Bryant (1935), Kirk (1947) and previous workers mentioned by him, and by Woodman (1948, 1949, 1950).

Some aspects of the aetiology and effects of onchocerciasis.

It is necessary to consider certain aspects of the aetiology and clinical effects of human onchocerciasis in order to understand the influence of *Simulium* on its distribution, to assess its importance, and to estimate the possible use of even minor anti-*Simulium* measures in a country where major control measures are impracticable.

Aetiology.

After microfilariae of *O. volvulus* have entered the insect host many of them die and those that survive do not multiply, so that only a few, about three, reach the infective stage in the insect's head. One or more of these may enter a man, and its subsequent fate until it becomes mature, is unknown, as Van den Berghe (1941a) points out. He also remarks that the worms probably only migrate a short distance. Hegner and others (1938, p. 449), discussing *Wuchereria bancrofti*, which has an essentially similar life history, point out that the two sexes may fail to meet, so that a human host may harbour adult parasites without microfilariae being produced. They remark that " successful infections are only the result of mass biting " and point to " the spotted geographic distribution of this and related species ".

Clinical effects.

The adult worms and their offspring, the microfilariae, both produce symptoms, many of which, however, cause little inconvenience. The adult worms often give rise to subcutaneous nodules. The microfilariae live mainly in the skin and often cause dermatitis in the forms of xeroderma, and sometimes pachyderma. Kirk (1947) found several lipomata during onchocerciasis surveys and recorded that hydrocoele and elephantiasis were extremely common in the infected areas.

Blindness is by far the most important effect of onchocerciasis but it only occurs in a small percentage of the infected population, from less than 1 up to about 10 per cent. Furthermore Buckley (1949), working in the area of *Simulium neavei* Roubaud (admittedly a species very different from *S. damnosum*) in Kenya, considered that only people living there for many years risked incurring blindness, and found that older people were the principal sufferers from clinical effects of onchocerciasis. Kirk pointed out that the factor leading to blindness in the Sudan was unknown but expressed the hope that control of *Simulium* in hyperendemic foci " might greatly reduce hyperinfestation, and with it, perhaps, most of the serious clinical manifestations of onchocerciasis ".

Discussion.

It is evident that, generally speaking, mass biting is necessary to produce the disease, or perhaps those symptoms that are caused by microfilariae, and that prolonged exposure or infection is necessary to produce the serious, ocular, symptoms. It will be seen that the disease only occurs in the Sudan in places where *S. damnosum* is abundant and not in all of these.

We do not know how many infective bites one can receive or how long one can remain unprotected against biting, in an infected area without serious risk, but it does appear that a limited number of infective bites often do little or no harm. Hughes and Sarkies (1951) point out that infants have been known to develop onchocerciasis, but their finding that " five years is sufficient for most adults to develop microfilarial infestation " shows that people can survive many infective bites unharmed. Dampf (1942) mentioned people living long in infected areas in America without becoming infected, and Strong and others (1934) pointed out that some people who were presumably infected several times a day only developed two subcutaneous nodules. At Mvolo dissections have shown that a person might receive hundreds of worms in a season, yet by no means all the inhabitants show microfilariae in the skin, and the same is probably true of many other places. It is a matter of common experience in the southern Sudan that many people visit onchocerciasis areas without afterwards showing any obvious symptoms.

The possible existence of an animal host.

Several authors have referred to the possibility that *O. volvulus* might exist in an animal reservoir, and if this were so it would affect control measures. According to Buckley (1949) there is no reason to presume that no animal reservoir exists. The skin of a single baboon was examined at Mvolo but no microfilariae were found.

Distribution of onchocerciasis.

Fig. 3 shows approximately the distribution of the disease according to the studies of the above-mentioned writers and the results of recent dissections of *Simulium*. In the Nile basin onchocerciasis occurs in a roughly crescentic area. The eastern part of the crescent may be mainly in Ethiopia, with a fringe in the Sudan. The southern part is in Uganda and the western part in the Sudan. In this, the main Sudan area, the disease occurs on the middle reaches of the southern rivers after they become big enough to breed *S. damnosum* in large numbers and before they enter the swamps. The L-shaped River Sue produces these conditions over a considerable distance. The disease only occupies a part of the country inhabited by *S. damnosum* but the species occurs also in the northern Sudan and on some southern streams in the absence of the disease.

The infected stretches of rivers lie in country which has a long dry season and poor soil and is infested with tsetse flies (*Glossina morsitans* Westw.). The infected areas are north of the comparatively fertile country near the Nile-Congo divide, which includes the Zande agricultural scheme around Yambio, and they are south of the great pastoral plains of the central Sudan. The problem is to control the disease in a sparsely populated and mainly unproductive rural area. The town of Wau is slightly affected, and the educational centres of Bussere, Mundiri and Raffili are in the main *S. damnosum* area, but Mundiri, built in 1948, is at present unaffected although onchocerciasis has been reported downstream on the same river.

With regard to the relation between the disease and distance from a breeding place, Kirk made surveys between Raffili and the River Bo, which are near breeding places, and at Peili, 13 km. from the Sue. He found infection rates of 76 and 25 per cent. respectively. These findings may be compared with those of Wanson and others (1945) near Leopoldville. They found rates of over 90 per cent. near the main breeding place, 25 to 29 per cent. 10 to 15 km. away, and 14 to 15 per cent. 20 to 30 km. away. They also found that the infection rate was usually negligible in *S. damnosum* more than 12 km. from the breeding place.

The incidence of blindness in onchocerciasis areas in the Sudan, reported by Kirk (1947) and Woodman (1949), varied from less than 1 per cent. of people examined (at Mbiri's) to an estimated 10 per cent. of the population (at Pongo).

The place referred to as Wan Alel by Bryant is shown as Allel in fig. 3. The place called Basia by Kirk and Sue I by Woodman is shown as Maingbara, and that called Sue rest house by Kirk and Sue II by Woodman as Mbiri's.

Other species of Onchocerca.

Various species other than *O. volvulus* have been recorded from the Sudan and are mentioned here because some may be transmitted by SIMULIIDAE and because they must be borne in mind when examining *Simulium* for the *O. volvulus* infection rate. Mohammed (1931) reported *O. armillata*, *O. fasciata* and *O. gutturosa* in domestic animals. Cruickshank (1936) found *Onchocerca* in an antelope. Nagaty (1942) reported *O. gibsoni* in cattle. In the Sudan Veterinary Service Report for 1940 a suspected case of bovine onchocerciasis was reported from Khartoum, and in the report for 1945 (Sudan Veterinary Service, 1947) *O. cervicalis* is recorded from a horse in Kordofan. In England a species of *Culicoides* carries *O. cervicalis*,

TABLE III.

Rapid variations in the infection rate (developing *Onchocerca*) in *S. damnosum* at Mvolo.

Date	6 a.m. to 1 p.m.		4 p.m. to 6 p.m.	
July 1948	Number dissected	Percentage infected	Number dissected	Percentage infected
7	30	30·0	—	—
8	28	17·9	—	—
9	49	28·6	18	9·6
10	52	26·0	20	5·0
11	89	24·7	40	30·0
12	37	24·3	10	10·0
13	30	40·0	17	29·4
14	41	24·4	37	8·1
15	20	0	—	—

and *O. gutturosa* develops in *S. ornatum* (Steward, 1937). No microfilariae were found in the skin of a baboon which was examined at Mvolo.

Identification.

The appearance and measurements of microfilariae and developing larval worms commonly seen in *S. damnosum* correspond with descriptions of *Onchocerca volvulus* Leuckart. Since wild animals, except baboons, were not seen where flies were collected, and the flies took up microfilariae from the many infected people, the worms seen were assumed to be *O. volvulus*. It would be useful, however, to know if *S. damnosum* transmits other species of *Onchocerca*.

S. damnosum *as the vector of* O. volvulus *in the Sudan.*

The abundance of *S. damnosum*, the well-known vector of onchocerciasis, in the infected areas, its frequently high infection rate, and the absence of other man-biting species of *Simulium* indicated that *S. damnosum* was the vector. Observations were made, however, to confirm that the worm does develop in the local *S. damnosum* as Blacklock (1926a, b) in West Africa and Wanson and others (1945) in the Belgian Congo showed it to do.

Flies were caught at Mvolo in June, when the infection rate was not more than about 5 per cent., after they had bitten a heavily infected boy (the boy mentioned below in the section on numbers of *Onchocerca*). The flies were kept at about 24·5°C. and dissected when they died. After 1 day following the blood meal microfilariae were found in 68 out of 76 flies dissected. After 2 days microfilariae or early sausage forms were found in 49 out of 66 flies, and after 3 days in 36 out of 55. After 4 days sausage larvae were found in 11 of 29 flies, and after 5 days in five out of nine. After 6 days no worms were found in the two flies dissected. After 7 days vermiform *Onchocerca* were found in three out of five flies, and after 8 days in none of the two dissected. After 9 days worms were found in the one fly dissected. After 10 days vermiform larvae were found in the heads of all four flies dissected, and after 11 days similar forms in the one fly dissected. It was concluded that *O. volvulus* develops in *S. damnosum* as it does in West Africa.

S. griseicolle is the only other species that bites man in the Sudan but it does so rarely if ever in the *Onchocerca* region. Even if onchocerciasis were to reach the northern Sudan, where this fly does bite, it would be unlikely to transmit the disease because only a small proportion of the flies bite man.

The natural infection rate.

Flies were usually dissected 14 hours or less after capture. In considering the implication of high infection rates it is important to remember that, for reasons explained above, the risk run by a person in the presence of infected flies is not exactly known.

Rapid changes in the infection rates.

Table III shows that at Mvolo the infection rate could change rapidly from day to day and even during a single day, possibly owing to the changing proportion of young flies. It is evident that it may be necessary to remain for several days in one place to obtain a true picture of the infection rate there.

High infection rates.

There was a considerable infection rate at Mvolo during the rains, as seen from the 10-day averages shown in Table IV. The highest rate observed for 1 day was on 13th July when, out of 47 flies dissected, 36 per cent. were infected with developing forms and 8·5 per cent. contained worms in the head. Between 6 a.m. and 1 p.m., when 30 flies were dissected, 40 per cent. were infected, 10 per cent. with worms in

TABLE IV.

Numbers of *S. damnosum* dissected and found infected with developing *Onchocerca.*

Place*	Date	Number dissected	With sausage larvae	With vermiform larvae	With vermiform larvae in head	With double infections	Total	Percentage infected
	1948							
Mvolo	May 10–20	72	—	3	2	—	3	4·2
,, ...	,, 21–31	68	2	3	1	—	5	7·4
,, ...	June 1–10	193	9	2	1	2	11	5·6
,, ...	,, 11–20	264	4	5	2	—	9	3·4
,, ...	,, 21–30	328	2	3	1	—	5	1·5
,, ...	July 1–10	328	27	25	11	6	52	15·9
,, ...	,, 11–20	321	39	35	16	8	74	23·1
	1949							
,, ...	Aug. 11–20	109	6	11	5	2	17	15·6
,, ...	,, 21–31	59	3	8	5	1	11	18·6
,, ...	Sept. 1–10	56	7	6	2	—	13	23·2
,, ...	Nov. 11–20	84	—	—	—	—	—	0
Senango Faki...	Sept. 13	2	—	1	—	1	1	—
R. Sue near S. Faki ...	,, 13	18	1	3	—	—	4	22
Bandula ...	,, 16–18	76	1	—	—	—	1	1·3
Lubu	,, 20	60	—	2	—	—	2	3·3
Banga	,, 29	4	—	—	—	—	—	—
Mbiri's... ...	Oct. 5	42	1	—	—	—	1	2·4
Bakendi ...	,, 6	50	1	—	—	—	1	2
Maruko ...	Nov. 10	25	—	—	—	—	—	0
Total		2,159	103	107	46	20	210	

* Microfilariae were found at each place.

the head. These flies were collected near the river, 20 being caught on one person in 15 minutes, so that a man might have expected to be bitten by one infective fly in 7·5 minutes. With an average number of 2·5 worms per head infection this would imply a risk of infection with one worm about every 3 minutes. Some of the infection rates observed at Mvolo are very high compared with those from other parts of the world recorded by Van den Berghe (1941a). This is surprising in view of the fact that there are not very many inhabitants and not all of them are infected.

The distance of infected flies from rivers.

Dissections made at Mvolo and a few other places yielded useful information about the risk of encountering infected flies some distance from rivers. Of the flies dissected at Mvolo about half were collected near the River Naam and about half near the police station some 700 metres inland. The general infection rate and the rate for vermiform *Onchocerca* tended to be rather higher at the river, although only a few water carriers and other people visited the river during the rains. It may be that many flies become infected and then live for days or weeks among the thick riverain vegetation.

The discovery of *O. volvulus* in the head of a fly 11 km. from the Sue at Senango Faki, and of microfilariae in three out of four flies caught on people at Banga, 13 km. from the same river, demonstrated a risk of infection at least 11 km. from the river even at this point where it is comparatively small and is not known to have any rapids. Later, an infected fly was found at Mbiri's which is 19 km. from a lower part of the same river. There is a tributary nearer than this but *S. damnosum* is not known to breed in it.

Infected *Simulium* were also found at other points in the Sue valley near tributaries, at Bandula, Bakendi and Lubu, 23, 33 and 33 km. respectively from the main river. Pupae were found near Bakendi and Lubu. Whether the infected flies come from the river or a nearby tributary the practical conclusion is that they are to be found over a wide area. The result of Kirk's (1947) survey at Peili, 13 km. from Sue, suggests that the flies there are infected.

From these findings during brief surveys, together with the known distribution of the disease in the Sudan and the Belgian Congo, it is likely that there is in the Sue valley a belt of country some 400 km. (250 miles) long and from 24 to 70 km. or more wide in which people may be bitten by infected flies during the rains. Rather less extensive areas of infection probably occur along several other rivers, the total extent of such country amounting to thousands of square kilometres.

The season of transmission.

According to Kirk (1947) it has been commonly held that people became infected while fishing in rivers, which they do largely when the rivers are low or have ceased to flow. He doubted that this was the time of infection, and remarked that the main *Simulium* season occurred when the rivers flow rapidly and little fishing is done.

The dissections of *S. damnosum* at Mvolo (Table IV) in the rains of 1948 and 1949 during ten 10-day periods, already referred to, show that considerable infection rate persisted during this time, with an increase in July that may have been associated with a migration of small fish which attracted some fishermen. *Onchocerca* was found in the heads of flies in each period. As has already been mentioned (p. 615) *S. damnosum* is far more abundant and widespread during the rains than the dry season when it disappears altogether in many places. There may be some local transmission near certain rivers in the dry season, but there is no doubt that the main season of transmission must be during the rains.

There is also evidence that the infection rate in the fly diminishes in the dry season. On 15th November at Mvolo, when the dry season had begun, 84 flies were dissected and no *Onchocerca* found. This was in striking contrast to the rainy season. Nearly all the flies had clear halteres, and so were apparently a young population. This was probably due to the drier weather and the fact that burnt grass and sun-baked earth had replaced the verdant growth of a month before. The river had fallen but was still flowing and many people had come to fish, some camping by the water. Although the November observations were confined to 1 day they were so suggestive that they were continued on flies from Raffili where *S. damnosum* occurs throughout the year.

A total of 2,226 flies, collected monthly at Raffili between October 1950 and September, 1951 was examined. The year 1951 was unusually dry and, possibly for this reason, the number of infected flies was rather small to give conclusive results in view of possible errors involved in examining preserved flies. In the rainy season 13 infected flies were found among 1,363 examined. All except three contained vermiform larvae ; these three, which contained large sausage forms, were discarded for statistical purposes because sausage forms might have occurred in the dry season and been overlooked. In the dry season (November to April) 863 flies were examined and none was found to be infected. Mr. J. Taylor examined these figures statistically and found that the proportion of infected insects was significantly greater, at the 5 per cent. level, in the rainy season. If, in the dry season, more than 0·347 per cent. of all flies were infected, then the probability that a random sample of 863 flies would include no infected ones would be less than 5 per cent. It may therefore be concluded that in the dry season less than 0·347 per cent. of the insects were infected.

Flies were also collected at Raffili in February 1950 for other purposes, and a vermiform larva was found in one out of 151 examined. This finding probably indicates that transmission can occur in the dry season, possibly by flies living in some damp sheltered place.

Numbers of Onchocerca *in individual flies.*

The numbers of *Onchocerca* observed in *Simulium* provide information about the condition of people who have been bitten, the fate of the ingested microfilariae, and the number of larvae that may survive and infect another host.

Microfilariae.

As many as 1,000 or so microfilariae can be taken up by *Simulium* at a single blood meal (Strong & others, 1934, p. 108). It has been thought that the ingestion of large numbers of microfilariae by biting insects is made possible by an attraction of the parasites towards the proboscis (Craig, 1932 ; Vargas, 1942 ; and others). Gordon and Lumsden (1939) found that in the case of mosquitos the ingestion of numerous parasites might be due to another cause. D'Hooge (1934) considered that the number of *Onchocerca* found in the human skin was so large that the attraction theory was unnecessary to account for the numbers in the gut of *Simulium*. Whatever the reason, many microfilariae are taken up and 200 or more are frequently seen in the mid-gut of *S. damnosum* in the Sudan.

The number of microfilariae that may be taken up when a fly bites is very variable and depends on the intensity of infection of the person bitten, the area of skin selected and other factors. Some indication of the range of numbers is given by two series of approximate counts made at Mvolo.

One series was from 31 flies taken in July 1948 on a 12-year-old boy who had two nodules on the back of his head. Three of the flies contained no microfilariae, and four had large numbers, 100, 150, 200 and 200. High numbers are of a particular interest in relation to the fate of microfilariae which is discussed later. In the remaining flies the number varied from one to 80 and averaged 23·6 ; nine of these contained 25 or more and five had 50 or more.

The other series of approximate counts was made from flies biting various people in August 1949. In 58 flies which had ingested microfilariae, one fly contained 245 and another several hundreds. In the other 56 the number ranged from one to 60 with an average of 15·7, 12 containing 25 or more and five 50 or more.

An observation made incidentally was that the boy provided flies with fewer microfilariae in August 1949 than in July 1948. Of 18 flies that bit him in 1949, five were negative and none contained as many as 100. In the positive flies the number ranged from one to 60 and averaged 15·5. The averages in 1948 and 1949 were as follows : for all flies, 39·2 and 11·2 ; for flies with no worms or less than 100, 21·0 and 11·2 ; for infected flies with less than 100 worms, 23·6 and 15·5.

Developing larvae.

The stages at which larvae of *O. volvulus* are usually seen are determined by the fact that *S. damnosum* is usually caught while biting, which it does at more or less regular intervals after laying eggs. Three ovarian cycles correspond approximately to the period occupied by *O. volvulus* in developing from the microfilarial to the infective stage in the head. Larvae are therefore usually seen in one of three stages, small sausage larvae, large sausage larvae and vermiform larvae. It is desirable to dissect all flies immediately after capture but this is often impracticable, so it is usually better simply to record sausage and vermiform stages, as is done in Table V.

TABLE V.

Numbers of developing *O. volvulus* counted in *S. damnosum*.

	Stage of *O. volvulus* and site of infection	Max.	Mean	Min.	*Onchocerca* seen	No. of infections	No. of infected flies
Single infections	Sausage larvae (all in thorax)	10	2·5	1	251	101	101
	Vermiform larvae :						
	Thorax only... ...	8	3·1	1	134	44	44
	Thorax when others in abdomen and/or head	3	1·3	1	20	15	15
	Abdomen when others in thorax and head	2	1·5	1	6	4	
	Abdomen when others in thorax	2	1·3	1	4	3	
	Head when others in thorax and abdomen	5	2·0	1	8	4	
	Head when others in thorax	2	1·2	1	10	8	
	Abdomen when others in head	6	2·2	1	13	6	6
	Head when others in abdomen	12	3·8	1	23	6	
	Abdomen only ...	6	1·6	1	14	9	9
	Head only	7	2·3	1	64	28	28
Double infections (additional *O. volvulus* in same flies	Small sausage larvae...	—	—	—	9	1	—
	Large sausage larvae...	7	2·7	1	43	16	—
	Short vermiform larvae	5	4·0	2	12	3	—
Totals ...					611	—	203

/9

Mixed infections due to two infective feeds can often be recognised. In such instances the older lot of worms is shown as a single infection and the younger one as a double infection. When different stages were found and appeared to have originated from a single infection that stage was recorded to which most of the larvae belonged. Mixtures of large and small sausage forms were not usually differentiated in these observations. The number of sausage larvae seen in single infections was 251 and of vermiform larvae 296 ; additional larvae in double infections numbered 64, making a total of 611. The Table shows the distribution of these 611 larvae in 203 infected flies.

Several deductions can be made from the figures although there are some discrepancies due to inevitable delays between capture and dissection, the fact that some flies had died some time before dissection, and the occasional difficulty or impossibility of recognising double infections, particularly when two lots of larvae have reached the vermiform stage.

The number of larvae which complete their development in the fly from a single infection is best indicated by the average, 3·1, of those seen in the thorax when none had passed to the head or, as some do, to abdomen. The number in the head does not give the required figure because it is influenced by double infections and other factors.

This figure of 3·1 is much less than the average number of microfilariae ingested by a fly and there is a considerable loss after ingestion. None of this loss occurs during development in the thorax ; dead *Onchocerca* are never seen in this site and the average number of vermiform larvae counted is not less than that of sausage forms. It is in fact higher, probably because the smaller sausage forms are sometimes difficult to detect. This loss of parasites, which was observed by Wanson and others (1945), and is discussed in the section on movements of microfilariae, is evidently partially explained by the fact that one frequently finds dead microfilariae in the mid-gut between 1 and 2 days after a blood meal.

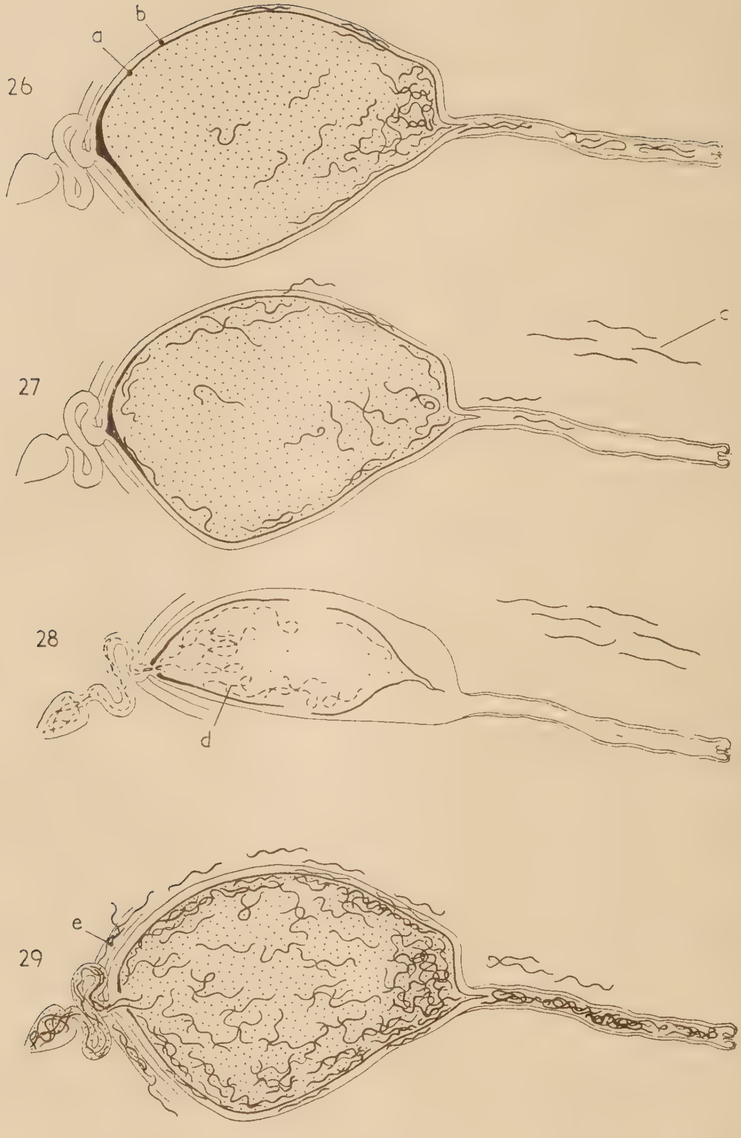
The number of worms in the head of the fly is of practical interest since it may determine the number which a man can receive when bitten. The average number found in the head was 2·3 but it is possible that in some instances a few had passed out of the heads of the flies when they were captured. The number present in the head at any one time is not simply the total number which had developed in the thorax as the result of one infective meal. Some of these may be ready to enter the head before the others. Some may enter the abdomen. The number in the head may be unusually large owing to a double infection or it may be the small remainder left behind after some infective worms have passed out of it. It appears that in many cases a fly may have to bite more than once before all its infective worms can reach a new human host.

With regard to the larvae in the abdomen it is interesting to note that Wanson and others (1945) sometimes found them in this site, and that Pratt and Newton (1946) observed that larvae of *Wuchereria bancrofti* migrated first to the abdomen and then to the head, some of them returning to the abdomen later.

Initial movements of microfilariae in the fly (figs. 26–44).

These movements were studied in order to find out what causes the above-mentioned death of many microfilariae and how the successful ones reach the thoracic muscles.

Although many microfilariae die it appears that most flies which take in the parasites do become infected with developing forms, since flies are easily infected experimentally, and very high natural infection rates are known. Evidently therefore there is a valve-like process which permits a limited number of the ingested parasites to develop.



Figs. 26–29.—Diagram showing the movements of microfilariae of *O. volvulus* in *S. damnosum* as deduced from the examination of sections and dissections: (26) immediately after a blood meal; (27) shortly after a meal; (28) 36 hours later; (29) immediately after a blood meal in a heavily infected fly in which microfilariae have passed into the hind-gut. (*a*) peritrophic membrane; (*b*) peritrophic space; (*c*) microfilariae in thoracic muscles; (*d*) dead microfilariae; (*e*) Malpighian tubes.

The path by which microfilariae reach the thorax has been discussed by Vargas (1942) and studied by him in South American *Simulium*. It appears that *S. ochraceum* takes up about 0·43 cu. mm. of blood, half of it in the oesophageal diverticulum, much in the expanding part of the mid-gut and some in the tubular part (in

S. damnosum it all enters the expanding part of the mid-gut). Vargas reported that in Hoffman's opinion the microfilariae passed very quickly through the mid-gut wall in *S. callidum* and *S. ochraceum*, none being found in the mid-gut 24 hours after feeding. Hoffman mentioned their occurrence in the thoracic muscles after 24 hours, and thought they might reach this position from the mid-gut either by passing out through the mid-gut wall or, if this were difficult to penetrate, by going *via* the cardia and oesophagus. Vargas considered that microfilariae in the mid-gut could not penetrate its walls and were all killed by digestive juices, or that, even if they escaped from it they would be barred from further progress for several hours by the pressure of the distended mid-gut against other organs. He thought that all microfilariae which reached the thoracic muscles probably did so by entering the oesophageal diverticulum and passing out through its thin walls to take up positions in the muscles in the vicinity.

The movements of another filarial worm, *Wuchereria bancrofti*, in a mosquito were studied by O'Connor and Beatty (1936) who found that 10 hours after a blood feed, but not earlier, microfilariae made their way forward from the expanding to the tubular part of the mid-gut. These authors concluded that some microfilariae passed through the wall of the expanding part of the mid-gut and thence to the thoracic muscles, and that a large number, later, passed through the wall of the tubular part to reach the same destination.

Microfilariae of *O. volvulus* in *S. damnosum* in the Sudan were studied in numerous dissections of fresh specimens and in a number of dissections and sections of preserved specimens.

Dissections of fresh flies.

Observations on very heavily infected flies are described in the last paragraph of this section.

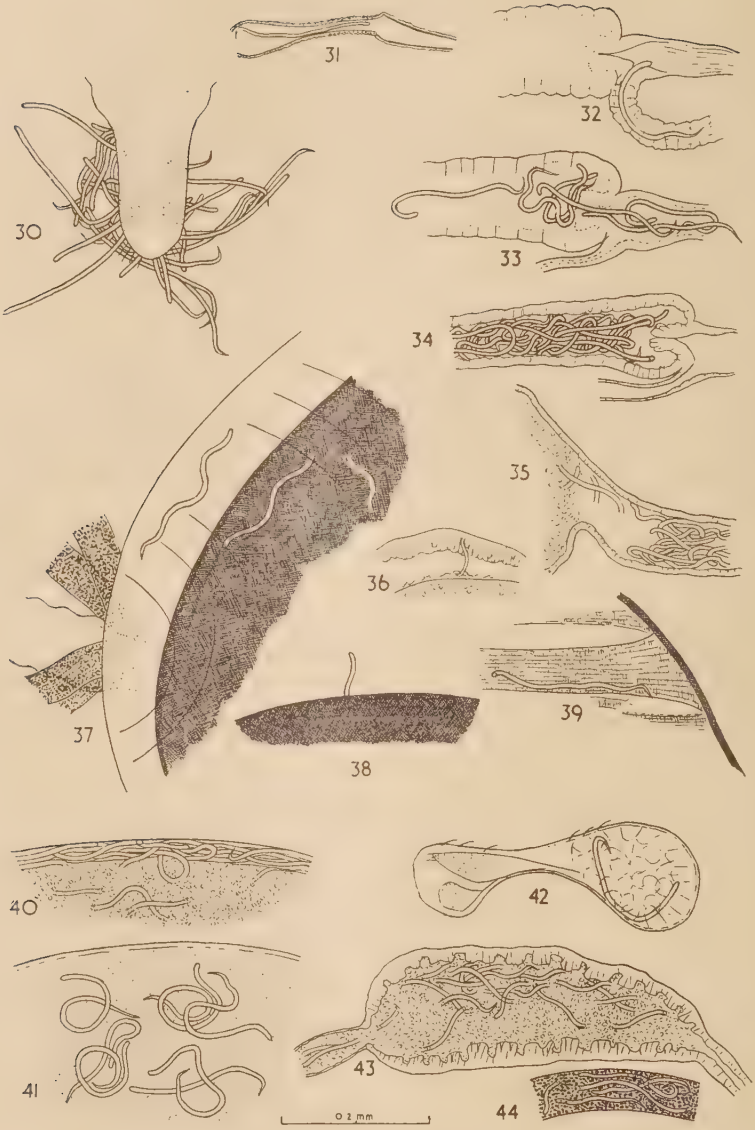
Microfilariae were often seen in the heads of flies from a few minutes to 6 hours after a blood meal. They appeared to be in the buccal cavity, pharynx and oesophagus, and often some emerged from the proboscis when a fly was crushed.

Particular attention was paid to the oesophageal diverticulum in view of Vargas's findings. A dead microfilaria was found in the duct of this organ in one fly (fig. 32). Otherwise no microfilariae were seen in the diverticulum except when it had broken during dissection and had apparently been entered by a few microfilariae afterwards.

A few or many microfilariae are often found in the tubular part of the mid-gut up to 6 hours after a blood meal (figs. 33–35). This observation was often made in flies with the blood mass intact, and therefore was not merely due to the escape of microfilariae during dissection.

In the expanded part of the mid-gut microfilariae are almost invariably to be seen in the blood within the peritrophic membrane after an infective blood meal (fig. 37). They tend to move to the periphery so that many are often visible, living or dead, in the membrane after the gut has been crushed and most of the blood has escaped (fig. 41). Microfilariae can remain alive in the membrane for many hours, and living ones have been seen in flies dissected 11, 14, 16, 20, 23 and 24 hours after a meal. Some on the other hand die much sooner ; dead microfilariae have been seen in the expanding part 7, 17, 20 and 48 hours after a meal. Dissections made between 24 and 48 hours after a meal indicate that microfilariae enclosed by the peritrophic membrane for any length of time normally die before it disintegrates. None of the many thousands found in the membrane during dissection was seen to penetrate it and it is almost certain that those that become enclosed by it eventually die.

About two or three microfilariae are often seen moving in the expanding parts of the mid-gut, in the peritrophic space and outside the blood mass and membrane (fig. 37). In one such instance a fly was dissected in normal saline 10 minutes after



Figs. 30–44.—Microfilariae of *O. volvulus* seen in dissections and sections of parts of *S. damnosum* captured while biting and killed later : (30) slightly crushed proboscis of fly which had bitten but not fed ; (31) oesophagus of fly which had just gorged ; (32) duct of oesophageal diverticulum with the only microfilaria (a dead one) ever seen in this organ ; (33) oesophagus and cardia ; (34) tubular part of mid-gut ; (35) junction of tubular and expanding parts at end of blood meal ; (36 and 37) expanding part 20 minutes after a partial meal ; (38) the expanding part with microfilaria apparently escaping ; (39) thoracic muscles three hours after fly had gorged ; (40) compressed peritrophic membrane four hours after a meal showing imprisoned microfilariae ; (41) membrane 19 hours after a meal with blood pressed out and dead and dying microfilariae left ; (42) haltere 210 minutes after fly had fed ; (43 and 44) mid-gut and Malpighian tubes of heavily infected fly in which microfilariae have rapidly passed to the hind-gut.

a small blood meal. Ten minutes after dissection water was added to the saline and the peritrophic space increased. Thirteen minutes later more saline was added and the space decreased so that the mid-gut wall came into contact with the peritrophic membrane (as it is in fully fed flies). Two minutes after this a microfilaria emerged from the dorsal surface of the distended wall of the mid-gut (fig. 38) and, after a further 2 minutes, another did so. They then remained attached to the outer surface of the mid-gut (which had been separated from other tissues) and crawled along it.

Occasionally microfilariae were found in the mid-gut of the flies which had been caught on people (up to 5 hours previously) but had not sucked blood. The flies had presumably taken up the parasites without probing long enough to break a capillary.

Microfilariae were sometimes seen in the hind-gut where they seemed to die much earlier than those in the mid-gut. In one fly dissected 6 hours after a blood meal there were 30 dead microfilariae in the hind-gut and 28 living ones elsewhere, two of them in the head, three in the tubular part of the mid-gut, 20 in the expanding part, and three in the thoracic muscles.

Microfilariae were sometimes seen not long after a meal in sites other than the alimentary canal. They were seen in the thoracic muscles 2 hours after a blood meal and after longer intervals (fig. 39). Sometimes one was seen in the anal region, apparently in the body cavity. One was found in a haltere (fig. 42) and its presence there is an illustration of the activity and burrowing power of the parasite.

In addition to the above observations, several flies were dissected which had ingested a very large number of microfilariae and in which some blood had passed into the hind-gut (fig. 43) soon after a meal (as described in the foregoing section on changes in the mid-gut). Many microfilariae were to be seen in the hind-gut, and sometimes several were excreted, 14 being found on one occasion in a single faecal droplet. Many were seen in the Malpighian tubes (fig. 44) which were writhing with the rapid movements of the parasites. Van den Berghe (1941a) has referred to a tropism leading *Wuchereria bancrofti* to the Malpighian tubes of its insect host, but in the case of *O. volvulus* it is probable that some microfilariae which have reached the fore-part of the hind-gut take the line of least resistance into the tubes. When these flies were dissected various organs were so rapidly invaded by microfilariae that one could not determine which they had entered before the death of the fly. The parasites were seen to burst through the walls of the Malpighian tubes and it seems likely that many of them do this when the fly is alive and then quickly spread to other parts of the body.

Examination of preserved flies.

Microfilariae, dead and stationary, were seen in many of the organs mentioned above, frequently in the tubular part of the mid-gut. Some were seen in the thoracic muscles of a fly killed 210 minutes after a blood meal. On three occasions a microfilaria was seen in one of the halteres, and, since halteres were not always examined, it may be that microfilariae not infrequently enter this organ.

Examination of sections.

The use of sections has the advantage that the position of a parasite can often be precisely determined, and the following findings confirm and amplify some of those made during dissection. On the other hand there is a limit to the number of sections which can be cut and examined, special methods must be used to cut through the mass of blood in the mid-gut, fragments of parasites can be overlooked, and (as Strong, 1937, remarked) *Acanthocheilonema perstans* may be mistaken for *O. volvulus*.

Microfilariae were found in the following positions.

0–5 seconds after blood meal.

1. Many in mid-gut (some blood in hind-gut).
2. One in oesophagus, many at junction of tubular and expanding parts of mid-gut.

15 minutes after meal.

3. Two in pharynx, many in tubular part of mid-gut.
4. A few in middle of tubular part of mid-gut.
5. Many in anterior part of peritrophic space.

45 minutes after meal.

6. In expanding part of mid-gut but not in tubular part.

1 hour after meal.

7. One in dorsal part of peritrophic space (in contact with the part of the epithelium from which a microfilaria was seen to emerge in one of the dissections described above), several in lateral part of same space.
8. Many at anterior end of tubular part of mid-gut.

1½ hours after meal.

9. In expanding part of mid-gut.
10. Many in anterior part of peritrophic space.

2 hours after meal.

11. In tubular and expanding parts of mid-gut, and some in hind-gut.

3 hours after meal.

12. Many in thoracic muscles and various parts of the abdomen and in mid- and hind-guts. (There was a large mass of blood in the hind-gut, and evidently this was one of the flies which had taken up very many microfilariae and failed to develop its peritrophic membrane.)
13. In expanding part of mid-gut.

5 hours after meal.

14. One in tubular part of mid-gut.

Discussion.

It is thought that flies which take up hundreds of microfilariae usually die after a short time, a possibility suggested by Blacklock (1926b). The parasites apparently prevent the complete development of the peritrophic membrane and so escape to various parts of the body. In some of these flies which died within a day of feeding many microfilariae were found in the head, and up to about 100 in the thoracic muscles. Such numbers have not been found in the muscles of flies that survived for two days or more, presumably because heavily infected ones die.

The following remarks refer to the majority of flies, which take up moderate numbers of microfilariae.

The question of the fate of the many microfilariae which fail to reach the thoracic muscles is readily answered by the above-mentioned findings of the dead and dying parasites in the mass of blood in the expanding part of the mid-gut. As Lewis (1950) pointed out they are imprisoned by the peritrophic membrane. A few others may die elsewhere in the gut.

The process by which microfilariae pass from the alimentary canal to the thoracic muscles is evidently one which, as explained above, usually allows some of the parasites to do so but also restricts the number in any one fly. In discussing what may be the usual route one must bear in mind that this may differ in different flies, and that different microfilariae may accomplish it at different times. This would explain the variation in size often seen in the sausage forms of a single infection, and the occasional presence of microfilariae in the tissues some days after a meal, as seen by Blacklock (1926b). It is certain that conditions in different flies vary considerably according to age of the fly, the amount of blood and number of parasites ingested, and other factors.

Passage through the oesophagus is unlikely because, although thin-walled, it is lined with chitin. Passage through the oesophageal diverticulum can be ruled out because living microfilariae have never been found in an unbroken diverticulum. With regard to Vargas's idea of the microfilariae passing through the thin-walled diverticulum rather than the thick-walled mid-gut, one may mention that the latter, when fully distended, is very thin and delicate and invariably bursts during dissection whereas the diverticulum is easily removed unbroken.

Microfilariae have been seen in the tubular part of the mid-gut hours after a meal so it seems unlikely that they can readily escape through its wall. The hind-gut seems an unlikely route for microfilariae because they are seldom seen in it.

It is thought that the microfilariae which are destined to reach the thoracic muscles enter the tubular part of the mid-gut, remain there when the peritrophic membrane is being formed, and later pass backwards to the peritrophic space, out through the distended part of the mid-gut wall (pressing against the peritrophic membrane with their hooked tails) and forward to the thorax. This view is consistent with the observations described above and would account for the easy passage of a small number of microfilariae out from the gut.

It is known that microfilariae of a frog parasite can hold their position in the small capillaries against the blood stream and sometimes progress against it (Gordon & Lumsden, 1939), and it seems likely that some microfilariae of *O. volvulus* can cling to the walls of the tubular part of the mid-gut until the blood has passed into the expanding part. Some, on the other hand, may pass forward from the expanding to the tubular part before the membrane is complete.

The work of Wigglesworth (1930) and Hoare (1931) on the peritrophic membrane of other Diptera suggests that microfilariae might pass through the membrane of *S. damnosum* when it is being formed and is still soft. It seems just possible that this may occur, perhaps at one of the points where it is thin.

In whatever way the successful microfilariae reach the thorax there is scarcely any doubt that they escape inclusion in the peritrophic membrane and that this structure limits their number.

The possibility of onchocerciasis spreading.

If the disease should spread it is likely to be carried by the vertebrate rather that the invertebrate host, since the latter contains few of the parasites.

The southern Sudan.

Bryant (1935) thought that onchocerciasis had spread to some extent, and it now appears to be established wherever the *S. damnosum* is abundant. At Farajok, Liwollo and Yei the fly is evidently not numerous enough to maintain transmission. Mundiri is apparently safe for the same reason but the fly might conceivably increase there.

The northern Sudan.

There are many places where *S. damnosum* is abundant and human onchocerciasis unknown. Owing to increasing economic development infected persons might reach these places but it is not known whether the flies could maintain transmission. Laigret (1929) found onchocerciasis in semi-desert country in the French Sudan, where *Simulium* apparently bred in occasional watercourses which only ran for a few weeks each year, and Anderson and Lehucher (1940) recorded onchocerciasis in North Africa. Khalil (1939), other writers mentioned by him, and Nagaty (1949) referred to a report of human onchocerciasis in Egypt, but according to Khalil (1938) this report was incorrect. As far as is known the disease does not exist in the Nile Valley north of about 9° or 10°.

In the northern Sudan *S. damnosum* breeds in the dry season, often in windswept country where there can be few resting places for adults. There is some evidence that transmission is much reduced in the south during the dry season and it may be that conditions are even less favourable to the parasite in the north. Most flies hitherto dissected at Wad Medani appeared to be too young to contain infective larvae. The fact that human onchocerciasis is not found in the north may mean that it cannot exist there. There may be no reason to fear a northward spread of onchocerciasis, but it is well to bear the possibility in mind in relation to movement of labour from the south.

Control.

Known methods of control.

No large scale means of control of onchocerciasis by drugs is at present known, and any effective control hitherto achieved has been due to measures against *Simulium*. For many years the control of Simuliids seemed virtually impossible. According to Bequaert (1934) " it is doubtful if any of the methods suggested are really satisfactory or economical." Strong (1938), referring to the importance and difficulty of controlling breeding, considered that Hissette's suggested 500-metre clearing would be of little use (at Kissende) and wrote of the value of modern residential centres in areas which could afford them. Van den Berghe (1941c) considered that *O. volvulus* could not be destroyed in the large human reservoir, that *Simulium* could not be controlled, and that clothes were the only means of partial protection for man. He concluded : " La prophylaxie de l'onchocercose est insoluble, l'association Simulie—homme ne pouvant être actuellement ni rompue ni deparasitée." Ridley (1945) referred to the great difficulty of control in undeveloped areas, and Strong (1944) considered that the provision of modern water supplies was the only satisfactory method in some areas.

This unhopeful position changed after the discovery of the new insecticides and in several parts of the world *Simulium* has been controlled by larvicides or by residual sprays applied to vegetation against adults.

Unfortunately, as is explained below, general control of *S. damnosum* in the Sudan is not practicable. The only thoroughly effective means of protection is the careful use of repellent by individuals, but nothing radical can be done to protect the general population. It is important, however, to bear in mind the nature of the disease; that the serious symptoms, although very serious, are found in comparatively few people and that even partial control measures may be of some use in preventing them. Various minor control measures are therefore discussed below.

Control of breeding.

Larvicides.—Extermination is impracticable owing to the immense cost which would be involved and the virtual certainty that *S. damnosum* would return from untreated areas.

Repeated application of larvicides in the rains would be very costly in materials, staff, labour, transport and road making, and might kill fish. The main rivers are large. Among those measured, the Pongo, Sue, Tonj, Gel, Naam and Yei were estimated to have an average daily flow, between May and October, 1942, of 2·9. 21·6, 6·5, 2·0, 2·4 and 9·7 millions of cubic metres respectively (Hurst & Black, 1945). The flow of the Sue in September was some 50 million cu. m.

Dams.—Damming rivers to control *Simulium* would be too expensive, but dams which may be built in the Northern Sudan for other purposes (Morrice, 1949) may have some effect on *Simulium* in that area.

Other methods.—At the Fola Rapids some natural factor prevents breeding but it is unlikely that it could be produced artificially elsewhere.

Destruction of adults.

It would be very expensive to apply residual insecticides to even a fraction of the infected area, and bush clearing would not prevent adults resting in herbage.

Methods of reducing the number of bites.

Clearing vegetation.—No clearing, however large, will prevent *S. damnosum* from biting, but the use of cleared watering places in the dry season might have some effect locally.

Removal from Simulium.—To remove villages to a distance at which people would receive no infective bites would mean evacuating large areas of country and is usually impossible owing to lack of water inland.

During the rains, when surface water is available inland, parties of hunters make expeditions away from the rivers. It might be practicable in some places for people to move inland during the rains and return in the dry season. In the northern Sudan many people migrate hundreds of miles each year to protect their cattle from biting flies. Wood-cutting gangs could be employed along rivers in infected areas during the dry season.

Siting new settlements.—People should live as far from infected rivers as is practicable. When examining a site for a new settlement it should be remembered that the numbers of *S. damnosum* can fluctuate from year to year. In one instance a centre was established at a time when *Simulium* were not noticed but they increased later. Wind, which is important at Leopoldville (Wanson & Henrard, 1945), is not sufficiently constant to influence the choice of site.

The use of buildings.—The protective value of even slightly darkened buildings has been mentioned above. Public buildings such as churches, court-houses and schools could be designed to give enough light for reading but enough shade to give considerable protection against *Simulium.*

Protective clothing.—Long trousers afford considerable protection and have been supplied to Government employees at Mvolo. *S. damnosum* has been found unable to bite through men's ordinary stockings.

Repellents.—Much information on modern repellents and their use is provided by Christophers (1947) and Dethier (1947). Travis and others (1946) describe successful tests with dimethyl phthalate against *Eusimulium pecuarum* (Riley). Liquid undiluted dimethyl phthalate was taken to Mvolo and applied direct to the skin, and was found to be so effective against *S. damnosum* that no other formulations or methods of application were tested.

Table VI shows the effect of applying the repellent to boys' legs from the knee downwards. When no precautions were taken to prevent the repellent being accidentally rubbed off (the boys' being allowed to return home after each catch) protection was good for seven hours and partial up to at least nine hours after application. The flies which did bite seemed to do so at a few points which had been rubbed, and, when this source of error was removed by re-applying repellent to these small areas at intervals, protection lasted 10 hours and probably more. These findings were

TABLE VI.

Numbers of *S. damnosum* biting boys' legs treated with dimethyl phthalate, in 20-min. exposure periods. Dosages of repellent are shown in cu. mm. per 100 sq. cm. of skin.

Hours after application	No precautions against removal by rubbing				Most rubbed points re-treated before each exposure	
	300 cu. mm.		130 cu. mm.		200 cu. mm.	
	Control	Treated	Control	Treated	Control	Treated
2	14	0	42	3	14	1
3	10	0	53	2	10	1
4	10	0	54	4	14	0
5	42	0	14	0	14	0
6	53	0	46	0	10	0
7	54	1	28	1	10	0
8	44	5	44	8	13	0
9	30	13	30	11	10	0
10	32	28	32	24	14	1

confirmed by every-day experience, the normal procedure being to apply repellent at sunrise and re-apply it occasionally at points like the elbows where it tended to rub off.

It seems not unlikely that *S. damnosum* may have tarsal sensory receptors and that the preliminary patting of the skin accounts for the high degree of repellency. The legs of treated boys were occasionally bitten just about the knee by flies which were repelled lower down, but few attacked the upper part of the body.

Practical experience of the efficacy of dimethyl phthalate against *S. damnosum* was gained by the writer's party of seven people who spent 80 days at Mvolo in the rains. *S. damnosum* bit the local inhabitants all day and every day, sometimes at the rate of more than 200 bites an hour, and many of the flies were infective. The party spent every day in the open air or in unscreened buildings and no special protective clothing was worn. On the average each person used 4·2 cc. of repellent a day, 5 cc. being a liberal allowance. It was advisable to apply repellent to exposed skin every morning and to carry a bottle of it in the pocket and re-anoint such areas as the elbows from which it is rubbed by furniture or clothing. With great care the number of bites could be reduced to less than five a month. The amount of sweating induced by moderate exercise did not remove repellent appreciably.

Dimethyl phthalate is supplied by the Sudan Ministry of Health for sale to the public at a low price as a public health measure against *Simulium* and several other insects. It is retailed in 4-ounce screw-topped bottles (at 75 milliemes) which can be converted into drop bottles by inserting a rectangular piece of wood or cork into the mouth.

The repellent is unlikely to be used adequately by the population in general, although it is very popular when made available owing to the relief from irritation which it affords. In practice it is likely to give partial protection to some people and complete protection to a few.

Summary.

Observations were made chiefly in the southern Sudan, particularly at Mvolo where human onchocerciasis is common. The country and climate are briefly described.

Methods are described at some length.

The distribution of *S. damnosum* and places where it is known to be abundant are shown on a map. It does not appear to exist at the Fola Rapids.

Changes in certain organs were studied, chiefly in relation to the approximate estimation of age and (particularly in the case of the mid-gut and peritrophic membrane) to the movements of microfilariae. Recently emerged flies can frequently be readily detected by the clarity of the halteres (in which glycogen has not yet been stored) and the presence of abundant fat body, and by less conspicuous features such as the absence of an old peritrophic membrane. The oesophageal diverticulum often contains plant sugars and particles of grit but never blood.

The peritrophic membrane is formed at the time of a blood meal by the epithelium of the expanding part of the mid-gut. It is a laminated chitinous envelope completely surrounding the blood and remains unbroken for 24 hours or more. When very large numbers of microfilariae are ingested they appear to prevent the completion of the membrane so that blood quickly passes to the hind-gut.

The main breeding season in the southern Sudan is during the rains when the rivers are in flood, and in the north it is in the dry season on a falling river. *S. damnosum* breeds mainly in rapids but also in quiet stretches of rivers. In the south the adults are widespread during the rains but restricted to patches of bush in the dry season. They probably live longer in the rains than the dry season but it appears that a few may live for a considerable period during the dry season. *S. damnosum* can probably fly or drift on the wind for 30 km. or more in the Sudan.

Material ingested by the female includes human blood and small particles of other tissue, plant sugar, microfilariae of *Onchocerca volvulus* and *Acanthocheilonema perstans*, particles of grit, and occasionally pollen grains.

Flies do not bite when the ovaries are developing, that is, not more than once in two or three days. They rarely if ever make interrupted blood meals. They bite in bush or open country and on level ground or hill tops, and in sunshine or under shady trees, but less in thick herbage than in the open. Very few flies bite in moderately dark buildings. Biting continues from before sunrise till after dusk but increases in the afternoon. One female can lay over 500 eggs.

Fifteen parasites other than *O. volvulus* were found : ~~five~~ Protozoa, six nematodes, a hymenopterous planidium larva, two mites and ~~an~~ unidentified bod~~y~~, the common ones being a species of *Mermis* (in the valley of the Sue) and the planidium.

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Human onchocerciasis occurs along the middle reaches of southern rivers before they reach the great swamps. It is much less widespread than *S. damnosum* which occurs without the disease in the northern Sudan and on southern streams. The infected area, although large, is relatively unimportant and unproductive, and no towns are seriously affected. The reported incidence of blindness ranges from less than 1 to about 10 per cent. of the population. *S. damnosum* is considered to be the sole vector.

At Mvolo during the rains the average infection rate of developing larvae in the fly was 12 per cent. The highest infection rate observed in one day was 36 per cent. with a head infection of 8·5 per cent. The highest figures for part of a day were 40 and 10 per cent.

Infected flies were found at various distances from the R. Sue up to 33 km. Some of these had bred in tributary streams but the findings showed that there is a wide belt along this river in which people can become infected. The rainy season is known to be the main season of transmission because at that time the fly is widely distributed and the infective stage of *O. volvulus* is common. In the dry season *S. damnosum* disappears from most infected areas. In the remaining infected areas it becomes scarce and restricted in distribution. There is evidence that the infection rate falls in the dry season, possibly owing to the effect of atmospheric conditions on the longevity of the fly.

The average number of microfilariae ingested is considerably greater than that of larvae (about three) which complete their development to the infective stage. Observations were made to find out what caused the mortality and how the successful parasites reached the thoracic muscles. It was found that most microfilariae become enclosed by the peritrophic membrane and stay in it till they die. Some remain in the tubular part of the mid-gut when the membrane is forming in the expanding part, and it is thought that a few of these pass into the peritrophic space, penetrate the epithelium of the expanding part of the mid-gut and make their way to the thoracic muscles. In very heavily infected flies some of the microfilariae appear to prevent the completion of the membrane, and force their way into the hind-gut up the Malpighian tubes from which they escape and probably spread to many parts of the fly and kill it.

The risk of onchocerciasis spreading north cannot be ruled out but there is no reason to think that it can become established in the arid northern Sudan.

Radical control of S. *damnosum* by larvicides is impracticable owing to the volume of the rivers and the size and nature of the country. Removal of villages from rivers is impracticable owing to the waterless nature of the country inland, but it might be feasible for people to move inland during the rains when surface water is obtainable and for wood-cutting gangs to operate only during the dry season. In siting new settlements it should be remembered that *Simulium* can fluctuate from year to year and the choice of sites should be based on experience of several years. The use of slightly darkened buildings and protective clothing is of some value. Dimethyl phthalate is very valuable as a repellent in the hands of a careful individual and can give complete protection. It is probably of little use to the general population but should protect some people.

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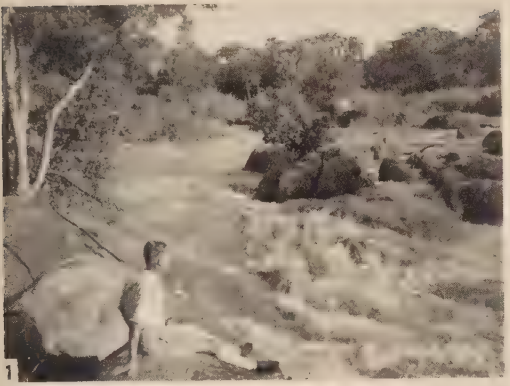
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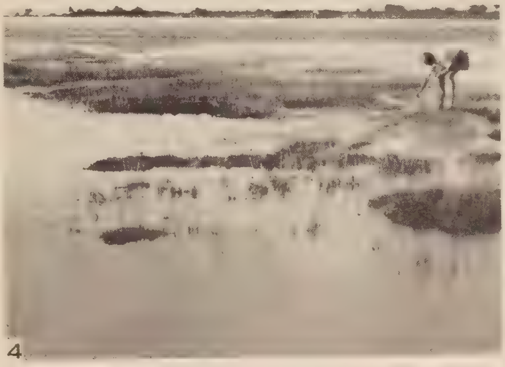
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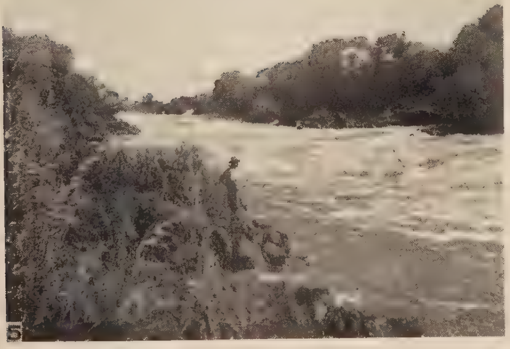
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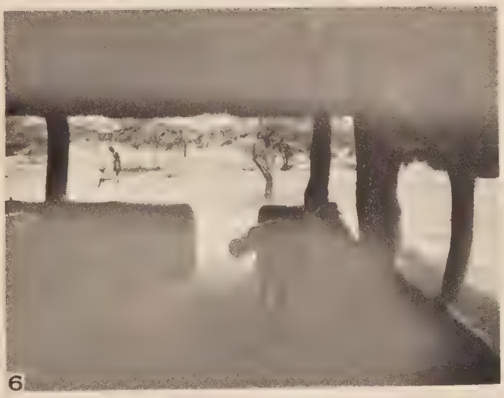
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FIG. 1. An arm of the River Naam at Mvolo where *S. damnosum* is abundant and heavily infected with *O. volvulus*.

FIG. 2. Mvolo, looking downstream from the rock seen in FIG. 1.

FIG. 3. A small stream at Liwollo, which is fast enough to breed *S. damnosum* but not big enough for adults to be in evidence.

FIG. 4. An example of a breeding place of *S. damnosum* where there are no rapids, the Blue Nile at Wad Medani.

FIG. 5. The Fola Rapids, one of the few rapids where *S. damnosum* is unknown.

FIG. 6. The rest house at Mvolo, showing the protection afforded by moderate shade. In half an hour the boy inside received one bite from *S. damnosum* and the boy outside 76.

A REVISION OF THE AFRICAN SPECIES OF *SESAMIA* GUENÉE AND RELATED GENERA (AGROTIDAE-LEPIDOPTERA).

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The Agrotid moths dealt with in this revision include some of the most important pests of graminaceous crops in Africa. It has previously been assumed that four species occur as stem-borers, namely *Sesamia calamistis* Hampson, *S. cretica* Lederer, *S. vuteria* (Stoll) and *Busseola fusca* (Fuller). The examination of a long series of adults reared from a variety of food plants during current investigations in the Gold Coast revealed not only that several distinct and apparently unnamed species were present but also that considerable confusion existed in the accepted nomenclature in the genus *Sesamia* Guenée, a great deal of which involved the species generally known as "*Sesamia vuteria* Stoll", which, apart from figuring prominently in the literature, was the supposed genotype of *Sesamia*. The settlement of the problem connected with this species required that several other species outside the genus *Sesamia* be studied; they are dealt with hereafter. Some other Agrotids reared from various grasses and cereals remain to be described, but are not included here since they do not affect the taxonomy of *Sesamia*. The genera and species considered in the present study are connected with the establishment of a correct nomenclature for the species of the genius *Sesamia*; most of them are of no economic importance themselves. *Busseola fusca* (Fuller), however, is included because it is part of the wider problem of stem-borers in Africa and is a major pest.

The material investigated consisted of the extensive collections of the British Museum (Natural History), which include type material of many of the species studied, and a large number of bred specimens from the Gold Coast.

Types of all new species described in the following pages are in the British Museum (Natural History).

Key to Genera considered in the present Paper.

1. Frons with pointed or rounded prominence..........2
   Frons without prominence..........5
2. Forewing with apex produced and acute, termen obliquely curved.......... *Speia*, **gen. n.**
   Forewing with apex rounded, termen evenly rounded..........3
3. Thorax clothed with hair and hair-like scales. Aedoeagus with apical bulbed cornutus or spinose. Bursa copulatrix without signum.......... *Poeonoma*, **gen. n.**
   Thorax clothed with hairs only..........4
4. Antenna of male bipectinate. Thorax with moderate crest. Male genitalia with valve simple, no sclerotised processes present. Bursa copulatrix with signum.......... *Sciomesa*, **gen. n.**

Antenna of male serrate. Thorax without crest. Male genitalia with valve possessing two heavily sclerotised dentate plates.........*Conicofrontia* Hampson

5. Thorax crested, clothed with hairs and hair-like scales. Male genitalia with valve entire, manica membranous, with bulbed apical cornutus on vesica. Bursa copulatrix with signum, ostial segment without a membranous pad before ostium ....*Busseola* Thurau

Thorax without crests, clothed with hair only. Male genitalia with valve entire or sacculus and cucullus separate, manica membranous or spinose, cornutus never bulbed. Bursa copulatrix of female without signum, ostial segment with a membranous pad before ostium..................................*Sesamia* Guenée

List of Genera, Species and Subspecies.

Speia, gen. n.

1. *vuteria* (Stoll)

Sciomesa, gen. n.

1. *mesoscia* (Hampson)
2. *mesophaea* (Aurivillius)
3. *scotochroa* (Hampson)

Conicofrontia Hampson

1. *sesamoides* Hampson

Poeonoma, gen. n.

1. *serrata* (Hampson)
2. *similis*, sp. n.
3. *acantha*, sp. n.

Busseola Thurau

1. *fusca* (Fuller)

Sesamia Guenée

1. *nonagrioides* (Lefebvre) p. 661
2. *botanephaga*, sp. n. 66
3. *madagascariensis* Saalmüller 663
4. *calamistis* Hampson 664.
5. *jansei*, sp. n. 666
6. *coniota* Hampson
7. *epunctifera* Hampson 667
8. *poephaga*, sp. n. 668
9. *penniseti*, sp. n. 669
10. *poebora*, sp. n. 670
11. *cretica* Lederer 6
12. *taenioleuca* (Wallengren)
13. *albivena* Hampson
14. *albivena sudanensis*, subsp. n.
15. *albivena mocoënsis*, subsp. n.
16. *rufescens* Hampson
17. *oviaula*, sp. n.*

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*This species is described separately at the end of the paper and is not included in the key.

Speia gen. n.

Genotype—*Phalaena vuteria* Stoll.

Proboscis aborted, small. Palpi obliquely upturned, the second segment reaching about to middle of frons and moderately fringed with hair in front, the third short, porrect. Frons with pointed conical prominence. Eyes large, round. Antenna of male bipectinate with short branches, serrate at apex, of female ciliate. Thorax clothed with hair only and without crests. Tibia fringed with rather long hair. Abdomen elongate, without crests. Forewing narrow and elongate, the apex produced and acute, the termen obliquely curved, not crenulate ; veins 3 and 5 from near angle of cell ; 6 from upper angle ; 9 from 10 anastomosing with 8 to form the areole ; 11 from cell. Hindwing with veins 3 and 4 from lower angle of cell ; 5 obsolescent from middle of discocellulars ; 6 and 7 from upper angle ; 8 from cell near base.

Male genitalia (fig. 53) : tegumen with small peniculi. Uncus large, with small apical hook. Valve large, elongate ; sacculus simple, cucullus small and bluntly rounded, not separated off from sacculus ; costal margin broadly sclerotised with a small ridge-like expansion which is not sclerotised. Aedoeagus short and stout, vesica with two strong cornuti, one dorsal and the other ventral, the upper margin convoluted. Juxta a simple, broad plate. Vinculum somewhat expanded ventrally.

Female genitalia (fig. 54) : ostium transverse, broad ; ovipositor lobes rather stout and broad.

The genus *Speia* is erected for Stoll's species *Phalaena vuteria*, which Hampson erroneously identified with *Cossus nonagrioides* Lefebvre, the species Guenée had cited as type of his genus *Sesamia*. Hampson sank *nonagrioides* as a synonym of " *vuteria* " and substituted the latter as genotype of *Sesamia*. It is difficult to understand this error since Stoll's description and figure were available to Hampson, the figure in particular showing that *vuteria* bears no resemblance to any species of *Sesamia*. Hampson did have specimens of *vuteria*, but described them as the male of his own species *Conicofrontia sesamoides*, from which *vuteria* is as distinct as it is from *Sesamia*.

Speia is more closely related to the genus *Sciomesa* described below than to *Sesamia*, judging by the structure of the genitalia.

Speia vuteria (Stoll) (figs. 60, 61, 62).

Phalaena vuteria Stoll 1783, Suppl. Cram. Pap. Exot., **5**, p. 161, pl. 36, fig. 5.

Conicofrontia sesamiodes (*sic*) Hampson 1910, ♂ only, Hampson, Cat. Lep. Phal. Brit. Mus., **9**, p. 338, fig. 152, *ex errore*.

♂. Palpus white, lightly infuscate. Antenna shortly bipectinate, serrate at apex, cilia short. Thorax white with light ochraceous suffusion anteriorly. Pectus white. Legs white. Abdomen white with light ochraceous suffusion. Forewing white with light ochraceous suffusion and irrorate with fuscous-black, with some fuscous-black markings ; two small fuscous-black points at base below costa and cell ; a fuscous-black spot at lower angle of cell with two very small streaks beyond the angle ; a curved postmedial fascia of one row of fuscous-black dots on the veins. Hindwing white, veins and termen slightly suffused with ochraceous. Underside of forewing white, costa and apex with slight ochraceous suffusion. Underside of hindwing white.

Expanse, 54 mm.

Male genitalia as for genus (fig. 53).

Female similar to male ; expanse, 54 mm. Genitalia as for genus (fig. 54).

South Africa : Natal, Durban.

Speia vuteria is easily recognised by its large size, the conical prominence of the frons and the elongate, ample forewings with their produced apex and oblique curved termen.

Sciomesa, gen. n.

Genotype—*Conicofrontia mesoscia* Hampson.

Proboscis aborted, small. Palpi upturned, the second segment reaching to just above the middle of the frons and moderately clothed with hair in front, the third short and porrect. Frons with pointed conical prominence. Eyes large, round. Antenna of male bipectinate, serrate at apex; of female ciliate.

Thorax clothed with hair only, the prothorax with a moderate crest, the tegulae inconspicuous but strongly crested. Tibiae fringed with long hair. Abdomen without crests. Forewing rather elongate, narrow, apex rounded and termen evenly curved, not crenulate; veins 3 and 5 from near lower angle of cell, 6 from upper angle or areole, 9 from 10 anastomosing with 8 to form the areole, 11 from cell. Hindwing with veins 3 and 4 from lower angle of cell, 5 obsolescent from middle of discocellulars, 6 and 7 from upper angle of cell or short stalked, 8 anastomosing with cell near base.

Male genitalia: Tegumen with peniculi small. Uncus long, simple. Valve elongate without clasper or clavus; sacculus simple, more or less rounded at upper edge, with an oblique sclerotised bar between it and cucullus, which is simple and rounded at apex; costal margin sclerotised, with a shelf-like expansion which has a more heavily sclerotised edge. Aedoeagus short and stout, manica entirely membranous; vesica with a basal ventral cornutus which is scobinate at its base and strongly toothed at its apex, and an apical beak shaped cornutus. Juxta plate-like, bifid. Vinculum somewhat dilate ventrally.

Female genitalia: Bursa copulatrix large and membranous; a pair of signa present, sometimes weak; ductus bursae sclerotised throughout and sharply differentiated from the bursa; ductus seminalis from bursa. Genital opening large and rounded with weakly sclerotised ventral lip, the ostial segment membranous throughout. Ovipositor lobes short and broad with many stout bristles in addition to the small setae and an apical crest of short stout bristles.

This genus is created for three species previously contained in the genus *Conicofrontia* Hampson. As shown in the discussion of the genus *Speia*, Hampson's later interpretation of *Conicofrontia* included two quite distinct genera due to his erroneous association of male and female under *Conicofrontia sesamoides*. The most widely known description of *Conicofrontia* being that in the Catalogue of Lepidoptera Phalaenae drawn up from the assumed male (*i.e.*, the male of *Speia vuteria*), it is natural that subsequent additions to *Conicofrontia*, being based on an incorrect diagnosis, should be more nearly related to the foregoing genus than to true *Conicofrontia*. *Sciomesa* is in fact very close to *Speia* but differs from the latter in that the species are much smaller, the antennae of the male strongly bipectinate, the thorax crested and the apex of the forewing not produced, the termen being evenly curved. The genitalia differ only in details.

The genus as here defined is restricted to South and East Africa. The biology is unknown.

KEY TO THE SPECIES OF SCIOMESA.

1. Forewing without distinct reniform spot, colour brown or fuscous-brown.........2
   Forewing with reniform spot, colour light buff to buff.........*mesoscia* (Hampson)
2. Forewing with medial longitudinal fuscous-black fascia, costal area distinctly paler than rest of wing. Bursa copulatrix with strong signa........................ *mesophaea* (Aurivillius)

Forewing without medial longitudinal fuscous fascia, costal area not distinctly paler than rest of wing. Bursa copulatrix with weak signum..................... *scotochroa* (Hampson)

Sciomesa mesoscia (Hampson).

Conicofrontia mesoscia Hampson 1918, Novit. Zool., **25**, p. 156.

♂. Palpus light buff, infuscate. Antenna strongly bipectinate, serrate at apex, cilia short fasciculate. Head light buff, slightly suffused with ochraceous and infuscate. Thorax light buff streaked with ochraceous, some fuscous suffusion at base of wing, tegulae with some fuscous streaking. Pectus light cartridge-buff, infuscate. Legs light cartridge-buff, infuscate, particularly the fore tibia. Abdomen white, suffused light buff. Forewing white, suffused with light buff and irrorate with fuscous, with distinctly pinkish iridescence, especially at base and along costa and termen ; medial vein and veins 4 and 5 white ; some fuscous to fuscous-black markings, variable in intensity ; a longitudinal fuscous-black fascia, sometimes fuscous-brown at wing base, extending along lower margin of cell, partly within the cell, partly without, to the postmedial fascia ; a black antemedial spot at base of cell ; a spot slightly more medial at upper margin of cell with a smaller spot slightly more distal ; a fuscous-black spot at lower margin of cell slightly more distal than the spots above the cell ; reniform spot white, defined with black on both sides ; a curved postmedial fascia of two rows of fuscous-black spots, the proximal row on the veins, the distal row interneural, but both rows sometimes coalesced to form a dentate line towards the inner margin ; a black spot just before apex ; an oblique subterminal fuscous suffusion from termen, just below apex, to about vein 2 ; a terminal series of black spots between the veins ; fringe infuscate, with white patches at vein endings. Hindwing white, infuscate to termen or nearly so ; an indistinct, curved, fuscous postmedial fascia and a terminal series of fuscous-black spots between the veins ; fringe lightly infuscate. Underside of forewing white irrorate with fuscous ; costa suffused light buff ; a broad fuscous suffusion medially with a large fuscous-black patch at apex of cell ; a terminal series of fuscous-black spots between the veins. Underside of hindwing white, irrorate with fuscous in terminal half ; costa suffused light buff ; a fuscous-black patch at apex of cell ; a curved fuscous postmedial fascia ; a terminal series of fuscous-black spots between the veins.

Expanse, 34 mm.

Male genitalia : as for genus ; the uncus somewhat diamond-shaped at apex ; valve with costal expansion without an inner point, sacculus rounded along upper margin ; aedoeagus with apical cornutus prominently beak-shaped.

Female similar to male, but with much more ochreous suffusion, particularly on the forewings where the fuscous markings, with the exception of the terminal series of spots, may be largely suffused with ochraceous. Expanse, 42 mm. Female genitalia as for genus ; bursa copulatrix very large with well developed signa ; ovipositor lobes with apex rather sharply rounded.

South Africa : Natal, Kloof, 1500. Northern Rhodesia : Gimson.

Sciomesa mesophaea (Aurivillius).

Conicofrontia mesophaea Aurivillius 1910, Kongl. Schwedischen Akad. Wiss., **9**, p. 31, pl. 1, fig. 6.

♂. Palpus whitish, with considerable fuscous irroration. Antenna bipectinate, serrate at apex, cilia short, fasciculate. Head strongly infuscate with some whitish anteriorly, more whitish with fuscous suffusion posteriorly with ochraceous-brown tufts at wing base. Pectus ochreous, suffused fuscous. Legs ochreous, tinged rufous, the anterior tibia infuscate. Abdomen light ochreous, suffused fuscous. Forewing ochraceous-brown, suffused pale ochraceous-buff along costa, with some fuscous to fuscous-black markings ; an antemedial fuscous-black spot at upper angle of cell ; an antemedial spot at lower angle of cell ; a longitudinal fuscous-black fascia from base, along lower margin of cell, partly within the cell partly without, extending almost to termen ; a fuscous-black spot at apex of cell with a smaller spot slightly more distal ; a postmedial fascia of two rows of fuscous-black spots, the proximal row on the veins, the distal interneural ; a fuscous-black terminal line, very faint at vein endings ; fringe whitish, strongly infuscate at tips. Hindwing white, the termen and to a less extent the inner margin, suffused with ochraceous-fuscous, with a darker terminal line more or less interrupted at vein endings ; veins outlined with fuscous-brown ; fringe pale ochraceous-fuscous, tipped with whitish. Underside of forewing ochreous along costa and inner margin otherwise suffused with fuscous and irrorate with fuscous-black ; a fuscous-black spot at apex of cell, and a terminal series of fuscous-black spots between the veins. Underside of hind-wing white suffused with ochreous along termen, costa more fuscous-grey ; an indistinct fuscous patch at apex of cell ; veins outlined with fuscous.

Expanse, 36 mm.

Male genitalia : very similar to those of *mesoscia* ; uncus not diamond-shaped at apex ; valve (figs. 1, 2) with sacculus less rounded, cucullus much blunter at apex, the costal expansion with a small inner point ; aedoeagus with apical cornutus less prominently beak-shaped.

Female similar to male, but sometimes forewing paler with the fuscous markings reduced ; expanse, 36–39 mm. The female genitalia differ from those of *mesoscia* in having a much smaller bursa copulatrix ; the ovipositor lobes are also more bluntly rounded at the tips.

NORTHERN RHODESIA : Gimson, 1908.

Sciomesa scotochroa (Hampson).

Conicofrontia scotochroa Hampson 1914, Ann. Mag. nat. Hist., (8) **13**, p. 164.

♀. Palpus buff, irrorate with fuscous. Antenna simple. Head ochraceous-buff streaked with fuscous, frons more heavily infuscate. Thorax ochraceous, almost golden-buff, sparsely streaked with fuscous anteriorly. Pectus light ochraceous-buff, laterally infuscate. Legs buff, fore tibia infuscate. Forewing buff-brown suffused fuscous-brown in terminal half ; with some fuscous markings ; a medial fuscous patch above the cell ; a postmedial spot between veins 5 and 6 with a smaller more proximal spot between veins 4 and 5 ; a fuscous, almost fuscous-brown, terminal line merging into the apical fuscous suffusion ; fringe infuscate. Hindwing whitish with light fuscous suffusion at apex, veins light ochraceous-fuscous, fringe lightly infuscate. Underside of forewing fuscous-brown, more ochraceous along costa. Underside of hindwing whitish, suffused ochraceous-buff at base, apex more fuscous with some fuscous irroration.

Expanse, 35 mm.

The female genitalia differ from those of both *mesoscia* and *mesophaea* in having a smaller ostium bursae and a smaller bursa copulatrix with insignificant signa.

Male unknown.

SOUTH AFRICA : Transvaal ; Natal, Mooi River.

Conicofrontia Hampson.

Conicofrontia Hampson 1902, Ann. S. Afr. Mus., **2,** p. 296.

Conicofrontia Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 338 (female only).

Genotype—*Conicofrontia sesamoides* Hampson.

Proboscis aborted, minute. Palpi upturned, porrect in female, the second segment reaching to just above the frons, the third short, porrect. Frons with a slightly conical prominence. Eyes large, round. Antenna of male serrate, of female simple, cilia short, fasciculate. Thorax clothed with hair only, without crests. Tibiae fringed with rather long hairs. Abdomen short, without crests. Forewing rather narrow, apex rounded and termen evenly curved ; veins 3 and 5 from near lower angle of cell ; 6 from just below upper angle ; 9 from 10 anastomosing with 8 to form the areole ; 11 from cell. Hindwing with 3 and 4 from lower angle of cell ; 5 obsolescent ; 6 and 7 from upper angle ; 8 anastomosing with cell only near base.

Male genitalia (fig. 55) : Tegumen with small peniculi. Uncus long, simple. Valve (fig. 3) elongate and narrow ; sacculus with heavily sclerotised and dentate clavus and the oblique bar across the upper edge of the sacculus produced into a heavily sclerotised dentate plate ; cucullus narrow, rather pointed at apex ; costal margin narrowly sclerotised and a small sclerotised ridge-like expansion. Aedoeagus short and stout, manica membranous, with paired and strongly dentate ventral cornuti. Juxta plate-like. Vinculum with a small ventral expansion.

Female genitalia (fig. 56) : Ostium with a comparatively simple armature, with two projections.

The confusion arising from Hampson's unfortunate association of the male of *Speia vuteria* with the female of *Conicofrontia sesamoides* has been discussed. The extent to which the later (1910) version of *Conicofrontia* supplanted that of 1902, the original, can be judged from the fact that Hampson described and correctly associated both sexes of *C. sesamoides* as *Phragmatiphila bipartita* in the Catalogue.

The present genus is in fact related to both *Speia* and *Sciomesa*. In the male sex, *Conicofrontia* can be separated from both genera by the serrate antennae and the very distinctive genitalia, which have a conspicuous clavus on the valve and large dentate cornuti on the aedoeagus. It may be distinguished in both sexes from *Speia* by its much smaller size and rounded wings, and from *Sciomesa* by the absence of a thoracic crest and the inconspicuously crested tegulae.

Conicofrontia sesamoides Hampson.

Conicofrontia sesamoides Hampson 1902, Ann. S. Afr. Mus., **2,** p. 296.

Conicofrontia sesamiodes (ex errore) Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 338 (female only) (recte *sesamoides*).

Phragmatiphila bipartita Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 266.

♂. Palpus white suffused light buff and moderately infuscate. Antenna serrate, cilia short, fasciculate. Head fuscous, streaked with buff. Thorax white suffused with light cartridge-buff and streaked fuscous to fuscous-black, particularly on the tegulae, producing a rather brownish general colour. Pectus infuscate. Legs white suffused pale buff and mixed fuscous. Forewing light cartridge-buff with considerable fuscous irroration which may be more intense towards termen ; some fuscous to fuscous-black markings, variable in extent and intensity ; a longitudinal, rather broad fuscous fascia from the base along the lower margin of the cell, partly within the cell, partly without, extending to just before the termen ; a fuscous-black spot at apex of cell ; a fuscous-black streak between veins 4 and 5 with another between veins 5 and 6 and a small black point between veins 3 and 4 ; a narrow fuscous terminal line interrupted at the veins and sometimes absent ; veins white towards termen ; fringe white with a medial fuscous line. Hindwing white, generally infuscate. Underside of forewing white, costal and terminal areas suffused fuscous. Underside of hindwing white, costal area suffused fuscous, medial vein outlined with fuscous.

Expanse, 27–30 mm.

Male genitalia : as for genus (figs. 3, 55).

Female similar to male, sometimes larger ; expanse, 30–36 mm. Female genitalia as for genus (fig. 56).

SOUTH AFRICA : Transvaal, White R. (type *bipartita*) ; Natal, Durban ; Cape Colony, Transkei (type *sesamoides*), E. Cape Province, Katberg.

This little species is easily separated from all the others dealt with here by the characteristic wing markings. Hampson's original spelling of the name, *sesamoides*, was altered for no apparent reason to " *sesamiodes* " in the Catalogue. It must be rejected for the original spelling.

Arenostola diamesa Hampson (Novit. Zool., **26,** p. 257, 1920) (**new comb.**) should be transferred to this genus. It is extremely close to *sesamoides*, but lacks the fuscous streaks between the veins.

Poeonoma, gen. n.

Genotype—*Phragmatiphila serrata* Hampson.

Proboscis aborted, small. Palpus upturned, the second segment reaching to about the middle of the frons, moderately clothed with long hair below, the third segment small, porrect. Frons with blunt prominence. Antenna of male serrate, of female simple, cilia short, fasciculate. Thorax clothed with hair-like scales and hair, without crests, but tegulae inflated, prominent and strongly crested. Tibiae fringed with long hair. Abdomen elongate, without crests. Forewing with apex rounded and termen evenly curved, not crenulate ; veins 3 and 5 from near lower angle of cell ; 6 from upper angle ; 9 from 10 anastomosing with 8 to form the areole ; 11 from cell. Hindwing with vein 3 from just before lower angle of cell, 4 from lower angle ; 5 obsolete from middle of discocellulars ; 6 and 7 from upper angle of cell or short stalked ; 8 anastomosing with cell near base.

Male genitalia : Tegumen with small or moderate peniculi. Uncus long, simple. Valve elongate, narrow ; sacculus with a small clavus, usually no more than a thin sclerotised edge but sometimes with small stiff hairs ; cucullus long, narrow, not separated from the sacculus ; costal edge narrowly sclerotised with a small ridge-like expansion. Aedoeagus short, inflated at base, manica entirely membranous, vesica with a long, apical, bulbed cornutus or armed with several rows of stout spines. Juxta simple, flat, vinculum moderately dilated basally with a small saccus.

Female genitalia : Bursa copulatrix large, without signum ; ductus bursae very long with a sclerotised reticulate pattern ; ductus seminalis from near apex of ductus bursae. Ostium large and broad, the anterior lip not sclerotised but with a sclerotised posterior plate.

The type species of this new genus was described by Hampson as a species of *Phragmatiphila*, but there are several discrepancies between *serrata* and typical *Phragmatiphila* such as *P. typhae* (Thunb.), notably the differently shaped frontal prominence, the presence of scales as well as hairs on the thorax and the lack of thoracic crests. *Poeonoma* is more nearly related to *Sciomesa* and *Speia* than to *Phragmatiphila* ; it differs from the first two in the shape of the frontal prominence, the serrate antennae of the male, the inflated tegulae and the presence of scales on the thorax. The male genitalia differ mainly in the form of the cornuti on the vesica ;

the female genitalia are more heavily sclerotised and the bursa copulatrix is without a signum.

Poeonoma contains two groups of species ; one, consisting of *serrata* and *similis*, sp. n., is characterised by the bulbed cornutus on the vesica of the male, and the other, containing at present only *acantha*, sp. n., has the vesica armed with several rows of stout spines. Whether a divergence exists between the females also is not known, the female of *serrata* only being known.

The genus appears to be predominantly West African ; although *serrata* was originally described from Ruwenzori it is widely distributed in the west and both the new species are western.

The larvae (only those of *P. serrata* are known) bore in grass stems. The eggs are laid in small to fairly large batches.

KEY TO THE SPECIES OF POEONOMA.

1. Forewing with subapical white points on costa ; antemedial and postmedial fasciae distinct. Male genitalia with bulbed cornutus on vesica..................2

   Forewing without subapical white points on costa ; postmedial fascia very weak or obsolete. Male genitalia with many rows of stout spines on vesica............ *acantha*, **sp. n.**

2. Forewing with subterminal series of white or ochreous-white points between the veins..*serrata* (Hampson)

   Forewing without subterminal series of white points between the veins............ *similis*, **sp. n.**

Poeonoma serrata Hampson.

Phragmatiphila serrata Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 268. pl. CXLII, fig. 31.

♂. Palpus white suffused ochraceous and considerably infuscate. Antenna serrate, setose ; cilia short, fasciculate. Head fuscous-black mixed with ochraceous, white at vertex. Thorax fuscous-brown, scales on tegulae tipped with white, suffused with ochraceous posteriorly. Pectus fuscous. Legs fuscous-black, tarsi with white rings at tip of each segment, white ventrally. Abdomen ochreous, suffused fuscous, anal tuft more heavily infuscate. Forewing ochreous, suffused and irrorate fuscous-brown at base, through cell and broadly along termen, an area from apex obliquely to inner margin and thence to base suffused light fuscous ; orbicular spot light fuscous, indistinct ; reniform spot white, defined on both sides by fuscous-black ; two subapical ochraceous-white spots on costa ; an oblique, slightly waved, fuscous-black antemedial fascia ; postmedial fuscous-black, curved outwards below costa, oblique and strongly dentate from vein 8 ; an oblique subterminal row of white spots between the veins, bounded on both sides by fuscous or fuscous-black ; a terminal series of interneural black spots which are suffused with white on inner margin ; fringe infuscate with narrow white basal and subapical lines. Hindwing light ochreous suffused fuscous, the veins outlined with fuscous-black ; fringe white suffused with light ochreous at base, otherwise lightly infuscate. Underside of the forewing generally suffused fuscous, costa irrorate with white and fuscous-black ; veins irrorate with white towards termen ; a fuscous-black patch at apex of cell and a terminal series of fuscous-black spots between the veins ; fringe ochraceous. Underside of hindwing ochraceous, suffused fuscous in costal half, irrorate with fuscous towards apex ; a fuscous spot at apex of cell and an indistinct fuscous postmedial line darkened to fuscous-black on veins 7 and 8 ; fringe ochraceous, white at tips.

Expanse, 28–35 mm.

Male genitalia : Valve (fig. 4) with costa fairly heavily sclerotised, costal expansion small but also moderately sclerotised. Vesica of aedoeagus (fig. 5) with a single bulbed cornutus which is scobinate at its base. Vinculum tapering gradually to a rounded point.

Female similar to male but sometimes considerably larger ; expanse, 35–46 mm. Female genitalia as for genus ; the posterior plate of ostial segment with a wedge-shaped projection into the ostium ; posterior apophyses with a large spoon-shaped expansion at their apices.

Uganda : Ruwenzori, 5,300. Gold Coast : Ashanti ; Kumasi, Mampong, Offinsu, Owabi, Wenchi. Nigeria : Ogruga (R. Niger).

Poeonoma serrata is superficially very similar, particularly in pale specimens, to *Busseola fusca* (Fuller). It is, however, easily separated from the latter by the presence of a frontal prominence in both sexes. It has been reared from *Pennisetum purpureum* from all the Gold Coast localities. Although this grass frequently grows in close proximity to maize, the larvae have never been found attacking the latter, although they will feed and develop normally on maize offered in the insectary. The larvae are dirty-white to black in colour, sluggish even when disturbed, and slow feeders. Pupation takes place within the stem, often in a small enlargement of the burrow ; the head of the pupa is downwards.

Poeonoma similis, sp. n.

♂. (Head and first two pairs of legs missing.) Thorax ochreous suffused and streaked with fuscous. Hind legs light ochreous, suffused with light fuscous, the tarsi with very indistinct whitish rings. Abdomen ochreous suffused fuscous, anal tuft ochreous. Forewing whitish heavily suffused and irrorate with fuscous-black ; traces of a fuscous-black dentate antemedial fascia ; reniform spot whitish defined by black ; a curved, slightly dentate, fuscous-black postmedial fascia ; a terminal series of small fuscous-black spots between the veins ; fringe light ochreous, irrorate with fuscous. Hindwing white, heavily irrorate with fuscous. Underside of forewing whitish, irrorate with fuscous along the costa, with some ochraceous suffusion medially ; termen suffused and irrorate with fuscous. Underside of hindwing whitish, irrorate with fuscous, particularly along the costa.

Expanse, 29 mm.

Male genitalia almost identical with those of *serrata*, but with the costa and costal expansion less heavily sclerotised, the vinculum straight-sided, then tapering rapidly to a point.

Female unknown.

S. Nigeria : Ibadan, 2.ii.1914 (*W. A. Lamborn*) (type ♂).

This species is very similar to *serrata*, but differs in being much darker, in the absence of an orbicular spot or a subterminal series of spots and in that the tarsi are not conspicuously ringed with white.

Poeonoma acantha, sp. n.

♂. Palpus fuscous to fuscous-black, streaked with white or ochreous-white. Antenna serrate. Head fuscous, streaked with ochreous at vertex and with a conspicuous ochreous-white patch below the frontal prominence. Thorax buff suffused with ochreous and heavily infuscate on the tegulae. Abdomen and anal tuft buff suffused with fuscous. Forewing buff suffused with ochraceous and with a slate-grey suffusion below the costa and along the termen ; orbicular and reniform spots ochraceous-white defined by black, the former drop-shaped, the latter followed by a fuscous-black discoidal spot ; a longitudinal fuscous fascia from base along lower margin of cell, partly within the cell partly without, extending to the terminal slate-grey suffusion ; an indistinct, curved, dentate, fuscous-black postmedial fascia ; a fuscous-black stripe between veins 5 and 6 and a smaller one between veins 4 and 5 ; a terminal series of fuscous-black spots between the veins ; fringe buff, infuscate at tip. Hindwing white, infuscate. Underside of forewing white, the costal area and termen suffused with light fuscous ; an indistinct fuscous-black spot at apex of cell. Underside of hindwing white, costa suffused with light buff and irrorate with fuscous, apex more fuscous ; a fuscous-black discoidal spot.

Expanse, 30–32 mm.

Male genitalia : Valve (fig. 6) with the sclerotised bar of the sacculus extended into a bluntly toothed apical process ; some small stiff hairs in region of clavus ; costal expansion large and strongly sclerotised. Aedoeagus (fig. 7) with the vesica armed with many rows of short stout spines.

Cameroons : Upper Uelle District, Dungu, April (type ♂). One male paratype with same data as type ; a second male paratype—Cameroons : Bitji, Ja R., 2,000 feet (Wet season) iv–v.1912 (*G. L. Bates*).

This species is easily separated from both *serrata* and *similis* by the pattern of the forewings and particularly the remarkable spinose vesica of the aedoeagus.

Busseola Thurau

Busseola Thurau 1904, Berl. ent. Z., **49,** pp. 55–58.

Calamistis Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 23.

Type species—*Busseola sorghicida* Thurau 1904 (by original designation).

Proboscis aborted, small. Palpus in male upright reaching to about level of vertex, in female oblique and reaching to middle of frons. Frons slightly inflated but without prominence. Eyes large, round. Antenna in male short-bipectinate, serrate at apex, in female simple, cilia short, fasciculate. Thorax clothed with hair and scales, without crests but with the tegulae rather prominently crested. Abdomen rather elongate, narrow. Forewing with apex rounded, the termen evenly curved, not crenulate ; vein 3 from apex of cell ; 4 arising very near 5 ; 6 and 7 from aerole ; 9 from 10 anastomosing with 8 to form areole ; 11 from cell. Hindwing with 3 from before angle ; 4 from angle ; 5 obsolete from below middle of discocellulars ; 6 and 7 with short stalk ; 8 anastomosing with cell near base only.

Male genitalia : Tegumen with small peniculi. Uncus simple. Valve broad ; sacculus rather narrow, without a distinct clavus, but with a heavily sclerotised, inwardly directed clasper from its upper margin ; cucullus small and narrow ; costal margin broadly sclerotised and produced into a heavily sclerotised spine. Aedoeagus short and stout, with paired lateral dentate processes at the level of the juxta ; vesica with a single long cornutus extending from its base almost to the apex where the cornutus is bluntly produced. Juxta simple. Vinculum slightly produced ventrally with a small bulbous saccus.

Female genitalia : Bursa copulatrix with signum ; ductus bursae broad, widening gradually into the bursa ; ductus seminalis opening into the base of the bursa. Ostium strongly transverse ; ostial segment with sclerotised plates anterior and posterior to the ostium. Ovipositor lobes short and relatively broad.

The genus *Busseola* was erected for an East African species, *B. sorghicida* Thurau. Several Ethiopian species have since been added to the genus, but of these, only one

B. fusca (Fuller), is known to attack cereal crops ; *B. fusca* is therefore the only species considered here.

Busseola, as represented by *B. fusca*, is probably most closely related to the *serrata* section of *Poeonoma*, an hypothesis supported by the close similarity of the larvae of the two genera. The genitalia of the male show an enlargement and sclerotisation of the valve and a reduction of the cornutus but are basically similar to those of *serrata*. Apart from the presence of a signum on the bursa in *Busseola*, the female genitalia differ only in the heavier sclerotisation in the present genus. The two genera have, in common, shortly bipectinate antennae in the male and the thoracic vestiture composed of scales and hairs.

The larvae bore in stems of cereals and grasses. They are very similar to those of *Poeonoma serrata*, but differ (judging from a study of those of *B. fusca*) in that seta L1 of abdominal segment 8 is separated from the spiracle by a distance greater than the width of its pinnaculum, the pinnaculi of all setae are less conspicuous, and the crotchets are smaller.

The eggs are laid in small to fairly large batches.

Busseola praepallens (Hampson) has been recorded as attacking maize in Southern Nigeria (Peacock, 1913). This may refer to a species of *Busseola*, but the insect in question was certainly not *praepallens*, which was described from Travancore.

Busseola fusca (Fuller)

Sesamia fusca Fuller 1901, First Rep. Govt. Ent. 1899–1900, Pietermaritzburg, p. 45, pl. xi.

Sesamia fusca Fuller, Hampson 1902, Ann. S. Afr. Mus., **2,** p. 296.

Calamistis fusca Fuller, Hampson, 1910, Cat. Lep. Phal. Brit. Mus., **2,** p. 274, fig. 116.

♂. Palpus light ochreous, moderately to heavily infuscate. Antenna bipectinate, serrate at apex, cilia short, fasciculate. Head ochreous, lightly to heavily infuscate. Thorax with fuscous suffusion anteriorly. Pectus fuscous. Legs ochreous, tibiae moderately infuscate, tarsi with white rings. Abdomen ochreous, variably infuscate. Forewing red-brown, suffused fuscous-brown over cell ; orbicular and reniform spots light ochreous with whitish annuli defined by black, but both sometimes absent ; a curved, dentate antemedial fuscous-black fascia ; a fuscous-black postmedial fascia, oblique from costa to vein 6 then dentate and oblique towards inner margin ; a fuscous stripe between veins 5 and 6 and another between veins 4 and 5 ; a subterminal fascia of interneural spots from vein 7 to 2, defined on the inner margin by wedge-shaped fuscous-black marks and on the outer side by faint fuscous marks between them and the terminal series of interneural fuscous-black spots ; fringe infuscate with a light ochreous basal line. Hindwing white suffused with light ochreous, and irrorate with fuscous particularly on the veins. Underside of forewing white suffused with light ochreous and irrorate with fuscous at apex and along termen ; an indistinct fuscous lunule at apex of cell ; a fuscous-black postmedial fascia darkened to black on costa. Underside of hindwing white suffused with light ochreous long costa, and irrorate with fuscous at apex ; a fuscous-black spot at apex of cell and an interrupted fuscous postmedial fascia.

Expanse, 26–34 mm.

Male genitalia as for genus : both the costal spine and the clasper are rather variable in shape, particularly the large tooth-like projections from the clasper (figs. 8, 9, 10) ; the cornutus of the vesica is scobinate and bluntly toothed at its apex. Juxta, fig. 11.

Female similar to male but sometimes darker. Expanse, 30–44 mm. Female genitalia as for genus : signum of bursa copulatrix narrow and finely scobinate ; ductus bursae heavily sclerotised basally with a lateral extension reaching almost to the bursa. The sclerotised plates of the ostial segment broad and rectangular.

Cape Province. Natal. Rhodesia. Tanganyika. Nyasaland. Kenya. Angola. French Guinea. Cameroons.

Nigeria : Western Provinces ; Ibadan. Northern Provinces ; Kano, Samaru nr. Zaria, Jos. Gold Coast : Gold Coast Colony ; Naswam. British Mandated Togoland ; Kpeve. Ashanti ; Mampong, Ejura, Wenchi. Northern Territories ; Tamale, Damongo, Lawra.

A series of specimens from the Gold Coast (Kpeve and Tamale) differs rather markedly from typical *fusca* in the following respects.

♂ and ♀. Generally very heavily infuscate ; head and thorax fuscous-black to black, lightly streaked with light ochreous or white. Forewing fuscous-black to black with some ochraceous suffusion at base and obliquely from apex to inner margin; veins 3 to 5 white from cell, veins 2 to 10 white at termen.

The male and female genitalia are identical with those of normal *fusca*. These specimens apparently represent the generation emerging following the onset of the early rains.

B. fusca is widely distributed throughout the Ethiopian Region, and is probably the best known of the African stem-borers, having been recognised as a major pest ever since the publication of Fuller's original description of the moth and its life history 50 years ago. Jepson (1951) states that it is most destructive in the drier parts of the African savannah ; so far as West Africa is concerned, it is probably more correct to say that it is most serious in the wetter areas of the Tree Savannah* and is less important in or even absent from the drier region of the Thorn Scrub Savannah*. It does not appear to occur at all in the southern rain-forest country.

Recorded food-plants are maize and millets among cereals ; Wilkinson (1936) records *Pennisetum purpureum* in Tanganyika, but states that all larvae in it died before pupation. Jepson (1951) found larvae in *P. purpureum* and *Panicum maximum* in Uganda. In the Gold Coast, it has been reared from the egg on *Rottboellia exaltata*.

Sesamia Guenée

Sesamia Guenée 1852, Hist. Nat. Insectes, Lépidoptères, **5,** Noctuélites i, p. 95.

Genotype—*Cossus nonagrioides* Lefebvre (monotypic).

Proboscis aborted, minute. Palpus upturned, the second segment reaching about to middle of frons and fringed with long hair in front, the third short. Frons smooth with a tuft of hair. Eyes large, round. Antennae of male bipectinate, shortly bipectinate or serrate, of female simple, cilia short, fasciculate. Thorax clothed with hair only, without crests. Tibiae fringed with rather long hair. Abdomen with long rough hair at base, but without crests. Forewing with apex rounded, termen evenly curved and not crenulate ; vein 3 from lower angle of cell or just before, 4 from lower angle or just after ; 6 from before upper angle or from angle, 7 from upper angle ; 9 from 10 anastomosing with 8 to form the areole ; 11 from cell. Hindwing with veins 3 and 4 from lower angle of cell or stalked, 3 sometimes from before angle ; 5 obsolescent from middle of discocellulars ; 6 and 7 from upper angle or stalked ; 8 anastomosing with cell near base only.

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* These terms are taken from Hutchinson and Dalziel 1936, *Flora of West Tropical Africa*, **2**, pt. 2, p. 603. They are not universally accepted, but are used here because the *Flora* is a widely known reference work. The boundaries of the vegetation zones shown on the map facing page 603 of it are at best only approximate and are in need of revision at several points.

Male genitalia : Tegumen with small peniculi. Uncus of moderate length, simple. Valve either with sacculus and cucullus separate, sacculus with an apical sclerotised and spinose process, cucullus narrow and spatulate, or with sacculus and cucullus not separate, the sacculus without an apical sclerotised process ; costal edge sclerotised with a strong dorsal spine of variable shape. Aedoeagus short and stout, manica membranous or spinose ; vesica with an apical flattened cornutus. Juxta of variable shape with or without a medial or dorsal projection. Vinculum expanded ventrally with a small saccus.

Female genitalia : Bursa copulatrix membranous, sometimes pointed at apex, without signum. Ductus bursae of variable length, distinct from bursa, with a variable degree of sclerotisation at base ; ductus seminalis from base of ductus bursae. Ostium more or less rounded or transverse ; a distinctive swelling, the ante-ostial pad, always present before the ostium, sometimes heavily pigmented ; ostial segment usually sclerotised, sometimes with large lateral plates occupying most of the sternum.

Although most of the species of this genus show a marked superficial resemblance to one another, a resemblance which has in the past led to a great deal of misidentification and confusion, a study of the male and female genitalia reveals good specific characters and also shows that the genus divides naturally into two groups ; larval characters indicate the same division. The first group, which includes the genotype, is characterised in the male by the separated cucullus and sacculus, simple juxta and membranous manica, and in the female by the larger and more rounded bursa, relatively narrower ostium and more or less well developed sclerotised areas on the ostial segment. The other (*cretica*) group is characterised in the male by the fused sacculus and cucullus (thereby connecting *Sesamia* with all the preceding genera), a medial or dorsal process to the juxta and the strongly spinose manica, and in the female by the more pointed bursa, broad ostium, frequently heavily sclerotised ante-ostial pad and the weakly sclerotised ostial segment. The two groups, though seemingly well separated are nevertheless linked by such forms as *S. jansei*, sp. n. and *S. coniota* Hampson which possess a partially fused sacculus and cucullus and a weakly spinose manica.

There is some difference in the geographical distribution of the *nonagrioides* and *cretica* groups, notably in that *nonagrioides* and its allies do not occur in eastern Europe, the Middle East, or north and north-east Africa, while the *cretica* group does not extend to western Europe, the Atlantic Isles, West Africa west of the Cameroons, and the Cape. The oriental species of *Sesamia* (*inferens* (Walker), *uniformis* Dudgeon, etc.) seem to be more closely related to the *cretica* group.

The larvae bore in the stems and heads of various grasses and cereals, and are usually of a pinkish colour. (The name " Pink Borers of Maize ", which is sometimes applied to these larvae, is rather unfortunate since larvae of *B. fusca* also are frequently decidedly pink.) *Sesamia* larvae are separable from both *Poeonoma* and *Busseola* by the fact that seta SD2 of abdominal segment 9 is practically in line with SD1 and L1, not distinctly set forward. Setae SD1 and SD2 of abdominal segment 8 are either anterior to the spiracle (*nonagrioides* group) or antero-dorsal to it (*cretica* group—see Cuscianna, 1935 ; Gardner, 1948).

The eggs are laid in small to large batches, inserted between the leaf sheath and the stem.

The confusion existing in the taxonomy of this genus has detracted from the value of much of the published work on this group of pests. Only one species, namely, *S. cretica*, has consistently been correctly identified ; in the following pages an attempt has been made to place correctly some of the more important references to the economically important species in the hope that it will stimulate further work on the bionomics and control of these insects, which include some of the most important pests of the African continent.

KEY TO THE SPECIES OF SESAMIA.

1. Antennae of male bipectinate or serrate for more than half the length of the antennal shaft. Male genitalia with sacculus and cucullus of valve separate, the former with an apical sclerotised process, the juxta simple and the manica usually membranous. Female genitalia with the ostium not strongly transverse, the bursa copulatrix broad and rounded and the ductus bursae long and narrow.......... 2

   Antennae of male simple, or serrate for less than half the length of the antennal shaft. Male genitalia with the valve entire, the juxta with a dorsal, medial or ventral process and the manica always spinose. Female genitalia with the ostium strongly transverse, the bursa copulatrix sometimes pointed and the ductus bursae short and broad.......... 20

2. Males.......... 3

   Females.......... 12

3. Manica of aedoeagus spinose.......... 4

   Manica of aedoeagus not spinose.......... 5

4. Forewing with median vein and veins 3 to 10 outlined with white, terminal line continuous..........*jansei*, **sp. n.**

   Forewing with median vein and veins 3 to 10 not outlined with white, with a terminal series of interneural black spots.......... *coniota* Hampson

5. Pectinations of antenna longer than the width of the antennal shaft.......... 6

   Pectinations of antenna less than the width of the antennal shaft.......... 10

6. Pectinations of antenna less than twice the width of the antennal shaft.......... 7

   Pectinations at least twice the width of the antennal shaft; costal spine of valve simple and pointed..........*madagascariensis* Saalmüller

7. Forewing strongly irrorate with fuscous and with a distinct longitudinal fuscous fascia along lower margin of cell.......... 8

   Forewing not strongly irrorate with fuscous and without a distinct longitudinal fuscous fascia along lower margin of cell..........*nonagrioides* (Lefebvre)

8. Genitalia with juxta short and broad, valve as broad as long, the costal spine short, little curved and almost bifid at apex..........*calamistis* Hampson

   Genitalia with the juxta flask-shaped with a long neck, the valve longer than broad, the costal spine long, curved and with a strong sub-apical tooth.......... *botanephaga*, **sp. n.**

9. Forewing with a continuous terminal line.......... 10

   Forewing with a terminal series of interneural spots.......... 11

10. Hindwing with veins 6 and 7 sessile. Forewing with considerable fuscous irroration..........*penniseti*, **sp. n.**

    Hindwing with veins 6 and 7 stalked. Forewing with very little fuscous irroration.......... *poephaga*, **sp. n.**

11. Forewing with three fuscous patches, one along upper margin of cell, a second along lower margin of cell, both within the cell, the third below the cell; wing without or with very little fuscous irroration..........*poebora*, **sp. n.**

    Forewing without three median fuscous patches and with considerable fuscous irroration..........*epunctifera* Hampson

12. Female genitalia with the last sternum strongly sclerotised, the base of the ductus bursae strongly sclerotised in longitudinal strips..........................13

Female genitalia with the last sternum not strongly sclerotised, with the base of the ductus bursae strongly sclerotised, the sclerotised area obliquely cut off distally, sometimes with a lateral extension into the ductus.................18

13. Sclerotised area of last sternum consists of two lateral, fairly narrow plates not produced posteriorly and not approximate in the mid-ventral line...........14

Sclerotised areas of last sternum produced posteriorly and approximate in the mid-ventral line.. 15

14. Forewing with considerable fuscous suffusion, veins 3 to 10 not outlined with white, vein 6 arising from angle of cell ; hindwing with veins 3 and 4 arising from lower angle of cell...*botanephaga*, **sp. n.**

Forewing with more ochraceous and less fuscous suffusion, veins 3 to 10 outlined with white and vein 6 arising before angle ; hindwing with vein 3 arising before angle..*jansei*, **sp. n.**

15. Forewing with a continuous terminal line..16
Forewing with a terminal series of interneural spots..............................17

16. Hindwing with veins 6 and 7 sessile..................................*penniseti*, **sp. n.**
Hindwing with veins 6 and 7 stalked...................................*poephaga*, **sp. n.**

17. Forewing decidedly yellowish with reduced fuscous markings and without or with very little fuscous irroration..................................*poebora*, **sp. n.**

Forewing pale buff or whitish with buff suffusion, not yellowish, and with considerable fuscous irroration.............................. *epunctifera* Hampson

18. Hindwing with veins 6 and 7 usually stalked. Ostium larger, the anteostial pad as broad as ostium..19

Hindwing with veins 6 and 7 sessile. Ostium small, the anteostial pad not as broad as ostium, the sclerotised area of ductus extensive and less obliquely cut off...*madagascariensis* Saalmüller

19. Sclerotised area of ductus prolonged into neck of ductus. Forewing more distinctly buff with reduced or obsolete fuscous markings.........................
nonagrioides (Lefebvre)

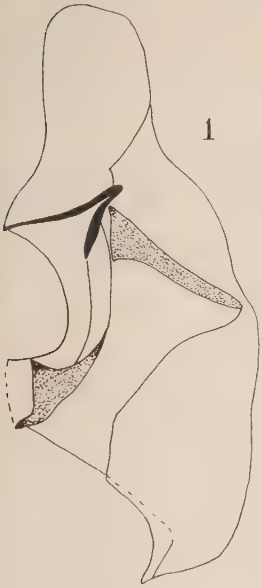
Sclerotised area of ductus not extended into ductus. Forewing usually more ochraceous with considerable fuscous suffusion and well developed fuscous fascia...*calamistis* Hampson

20. Forewing without rufous suffusion and not strongly infuscate along termen...21
Forewing suffused rufous and strongly infuscate along termen.....................
rufescens Hampson

21. Male genitalia with juxta small and with a small medial process. Female genitalia with anteostial pad small and not heavily sclerotised..................
cretica Lederer

Male genitalia with juxta large and with a long prominent medial or dorsal process. Female genitalia with the anteostial pad large and heavily sclerotised, the ostium markedly transverse...22

22. Forewing with a black spot at lower angle of cell. Male genitalia with vinculum broad, juxta with a large medial process..23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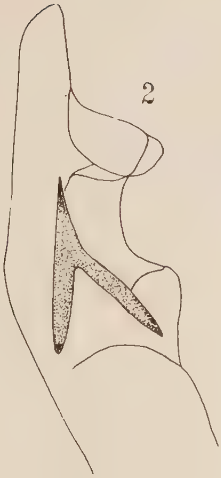
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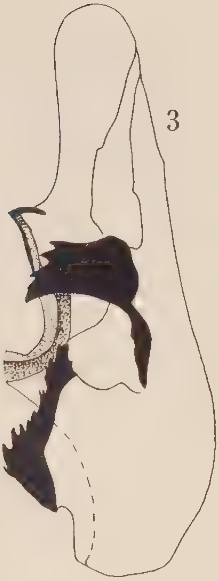
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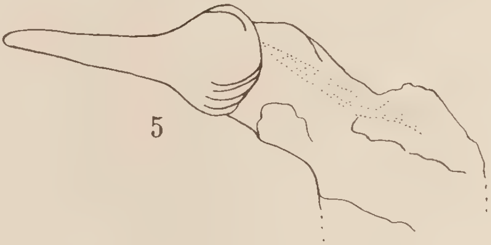
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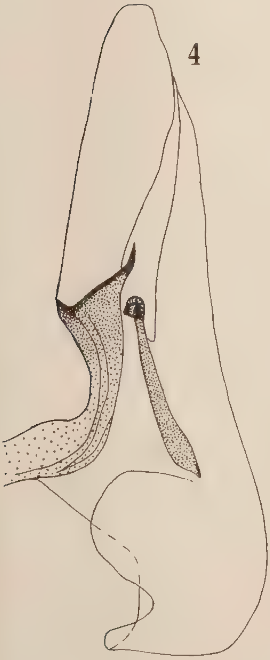
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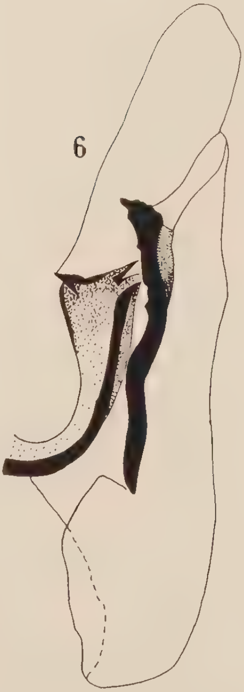
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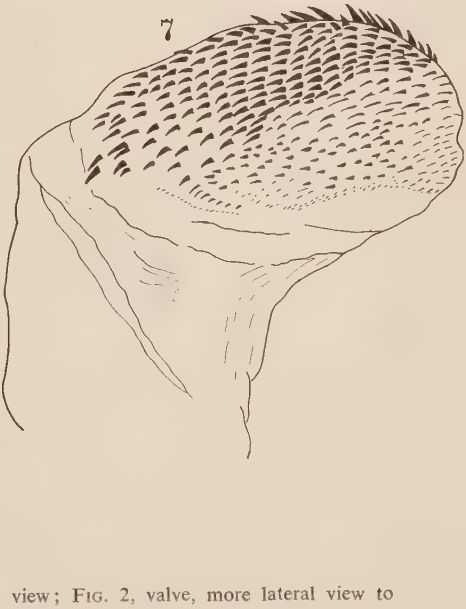
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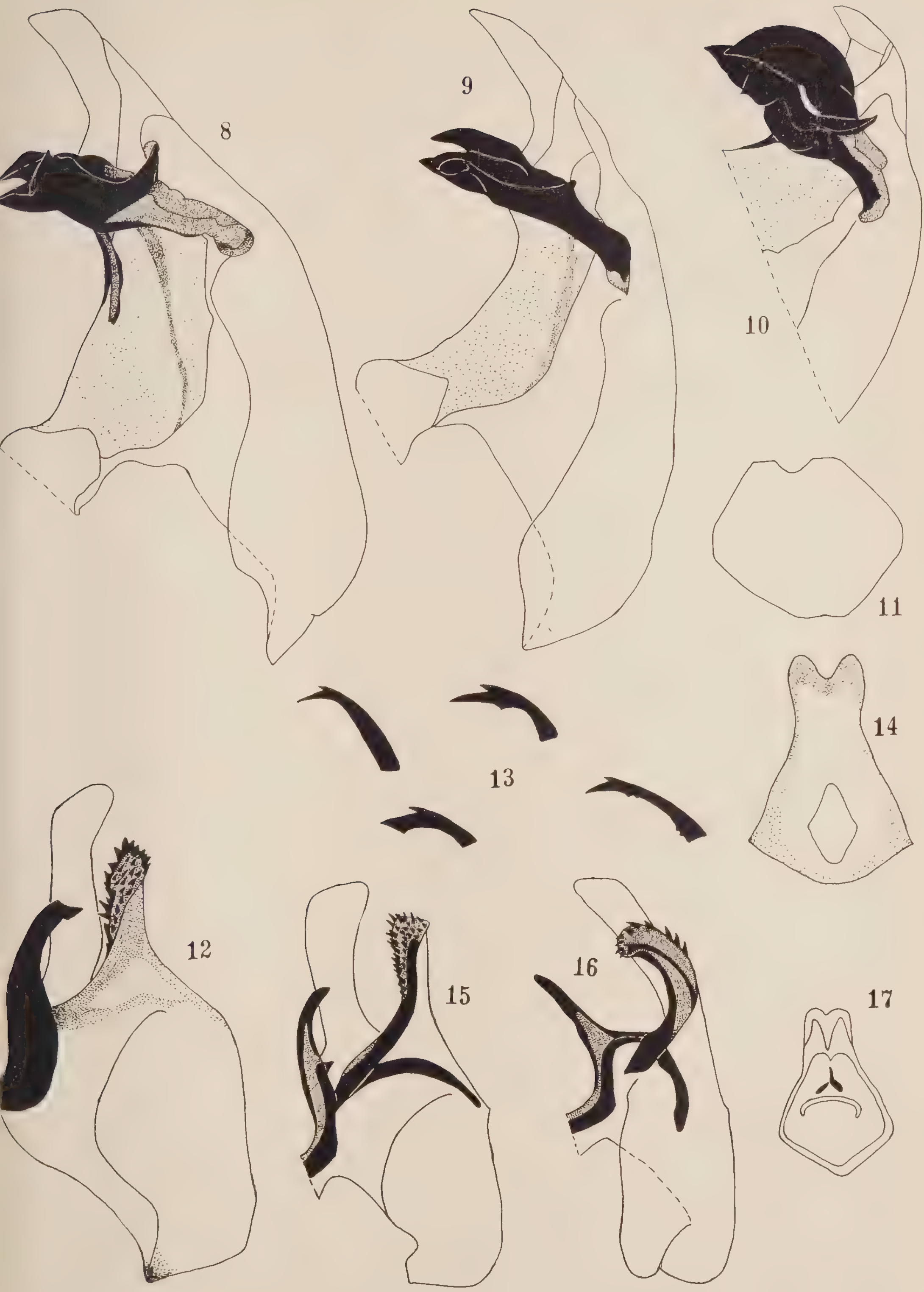
Sciomesa mesophaea (Aurivillius). Fig. 1, valve, ventral view; Fig. 2, valve, more lateral view to show costal ridge.

Conicofrontia sesamoides Hampson. Fig. 3, valve, ventral view.

Poeonoma serrata Hampson. Fig. 4, valve, ventral view; Fig. 5, aedoeagus, showing bulbed apical cornutus.

Poeonoma acantha, sp.n. Fig. 6, valve, ventral view; Fig. 7, aedoeagus, showing spinose vesica.



Busseola fusca (Fuller). Figs. 8, 9, valves, ventral view; Fig. 10, dorsal view of clasper and costal spine; Fig. 11, juxta, ventral view.
Sesamia botanephaga, sp.n. Fig. 12, valve, ventral view; Fig. 13, variation in costal spine of valve; Fig. 14, juxta, ventral view.
Sesamia madagascariensis Saalmüller. Fig. 15, valve, ventral view; Fig. 16, valve, lateral view; Fig. 17, juxta, ventral view.

Forewing without a black spot at lower angle of cell. Male genitalia with vinculum narrow, juxta with a long dorsal projection........................... *taenioleuca* (Wallengren)

23. Forewing not suffused with pink or only so at extreme base.......................24
Forewing suffused with pink......................................*albivena* Hampson

24. Thorax with some pinkish suffusion on humeri and sides of prothorax. Forewing with pinkish suffusion at base, terminal line usually black and prominent..*albivena sudanensis*, **subsp. n.**
Thorax without pinkish suffusion. Forewing without pinkish suffusion at base, terminal line more fuscous, less prominent.........*albivena mocoënsis*, **subsp. n.**

Sesamia nonagrioides (Lefebvre) (fig. 64).

Cossus nongarioides Lefebvre 1827, Ann. Soc. linn. Paris, **6,** p. 98, pl. 5.

Nonagria hesperica Rambur 1839, Faun. And., pl. 18, figs. 1–3.

Sesamia nonagrioides Lefebvre, Guenée 1852, Hist. Nat. Ins. Lépidoptères, **5,** Noctuélites i, p. 95.

Nonagria sacchari Wollaston 1858, Ann. Mag. nat. Hist., (3) **1,** p. 117.

Tapinostola gracilis Rebel 1898, Ann. naturh. Hofmus. Wien, **13,** p. 365.

Sesamia vuteria Stoll, Hampson (nec Stoll) 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 324, fig. 142 (in part).

Sesamia calamistis Hampson, Turati (nec Hampson) 1926, Atti Soc. ital. Sci. Nat., **65,** p. 42.

Sesamia vuteria Stoll, Mariani (nec Stoll) 1934, Boll. Soc. ent. Ital., **66,** pp. 184–188.

♂. Palpus cartridge-buff slightly irrorate with fuscous. Head buff. Thorax cartridge-buff, anteriorly suffused with buff. Pectus pale cartridge-buff. Legs cartridge-buff, fore tibia infuscate on inner surface, mid femur infuscate on inner surface. Forewing buff suffused with light ochraceous ; some fuscous markings variable in extent and intensity ; a very indistinct longitudinal fuscous fascia from base along lower margin of cell ; a fuscous patch about middle of discocellulars ; a curved postmedial fuscous fascia of one row of spots on the veins ; termen suffused pale fuscous ; a narrow fuscous terminal line ; fringe white, suffused with pale buff. Hindwing white with pale buff suffusion at apex ; fringe white suffused with pale buff along termen. Underside of forewing pale cartridge-buff suffused with ochraceous-buff along costa and termen. Underside of hindwing white, suffused with pale buff along costa, with some fuscous irroration along costa and at apex.

Expanse, 32–34 mm.

Male genitalia : Small ; tegumen with well developed peniculi. Uncus small, narrowing rather sharply at about halfway. Valve with sacculus and cucullus separate ; costal spine small with a small tooth some way before apex and sometimes slightly dentate at base ; apical extension of sacculus slightly broadened with several rows of short stout spines ; cucullus narrow, rather broadened at apex. Aedoeagus long, slightly dilate basally ; manica scobinate, the lateral lobes less so ; vesica with a small irregularly shaped subapical cornutus. Juxta rather rounded-conical, the base slightly produced to a blunt point. Vinculum with ventral expansion deep, without indentation.

Female similar to male, somewhat larger and frequently with much stronger buff suffusion ; expanse, 32–40 mm.

Female genitalia : Bursa copulatrix large ; ductus bursae long and narrow, with a basal sclerotised area obliquely cut off but with a lateral extension into neck of ductus. Ostial segment with weakly sclerotised, rather rectangular, lateral plates.

North-West Italy. Central and Southern France. Spain : Andalusia, Asturias, Galicia. Portugal. Azores : Madeira. Canary Islands : Gran Canaria, Tenerife.

Since Hampson's designation of *Phalaena vuteria* Stoll as genotype of *Sesamia* is invalid, the original citation of *Cossus nonagrioides* Levebvre by Guenée must be accepted.

As defined here, *S. nonagrioides* is a species of variable coloration, ranging from light buff to ochraceous buff with frequently reduced or obsolete fuscous markings. The genitalic characters, however, are constant ; this, together with the restricted distribution, should render identification a simple matter.

S. nonagrioides is a pest of some importance in maize in southern France and the Iberian peninsula. Feytaud (1923, 1931) and Genieys (1923) have worked out its life-history in France ; Delgado de Torres (1930) and Tavares (1928) give accounts of its depredations in Spain and Portugal, respectively. Figure 609 on page 803 of the compilation by Balachowsky and Mesnil (1936) refers to *S. nonagrioides*.

Recorded at present only from maize.

Sesamia botanephaga, sp. n.

♂. Palpus light cartridge-buff, lightly to moderately infuscate. Antenna short-bipectinate, serrate at apex, cilia short, fasciculate. Head light cartridge-buff, sometimes suffused with light ochraceous, lightly to moderately streaked with fuscous. Thorax light cartridge-buff, sometimes suffused with light ochraceous, sometimes almost white streaked with fuscous. Pectus white, infuscate at base. Legs light cartridge-buff, streaked with fuscous, fore femur infuscate on inner surface, fore tibiae suffused with ochraceous on inner surface. Abdomen white suffused with light buff and variably irrorate with fuscous. Anal tuft white, suffused with light buff and streaked with fuscous. Forewing light cartridge-buff, sometimes suffused with ochraceous, with considerable fuscous-buff to fuscous irroration, particularly along termen ; some fuscous to fuscous-black markings, variable in extent and intensity ; an antemedial fuscous-black spot below cell ; a longitudinal fuscous-black fascia from base along lower margin of cell, partly within, partly without cell, extending to wing margin ; a curved dentate postmedial fascia, extending from about vein 10 to vein 2, sometimes split into two postmedial rows of spots, the proximal on the veins, the distal interneural, a fuscous-black spot at the end of vein 1 on inner margin ; a narrow fuscous-black terminal line ; fringe with a narrow basal ochraceous-white line, infuscate medially and fuscous-white at tips. Hindwing white, veins sometimes with small fuscous-black stripes and apex sometimes irrorate with fuscous. Underside of forewing white, costa suffused buff, apex and terminal area suffused and heavily irrorate with fuscous to fuscous-black. Underside of hindwing white, costa and apex, termen sometimes, lightly irrorate with fuscous.

Expanse, 22–30 mm.

Male genitalia (fig. 57) very similar to those of *nonagrioides* but larger and stouter. Valve (figs. 12, 13) with costal spine large and curved with a prominent tooth before apex, sometimes dentate beneath apex and at base ; extension of sacculus larger, more heavily spinose, sometimes almost to costal spine. Aedoeagus similar to that of *nonagrioides* but vesica broadly sclerotised at base and without a distinct cornutus. Juxta (fig. 14) larger and broader.

Expanse, 22–38 mm.

Female similar to male ; expanse, 30–42 mm. Genitalia (fig. 58) with bursa copulatrix large, ductus bursae long and narrow. Ostial segment with two broad sclerotised lateral plates before ostium. Anteostial pad large, the ventral fold indented along the posterior margin.

Type ♂ : SOUTHERN NIGERIA : Ilesha (*Capt. Humfrey*).

Allotype ♀ : GOLD COAST : Kumasi (*J. Bowden*).

A large number of paratypes of both sexes from : IVORY COAST, Bingerville. GOLD COAST : Gold Coast Colony ; Abetifi, Aburi, Anyaboni, Asuansi, Axim, Bisa, Fosu, Mpraeso, Nkawkaw, Nsawam : Ashanti ; Ejura, Kumasi, Mampong, Offinsu, Sunyani : British Mandated Togoland ; Ho, Kete-Krachi, Kpandu, Kpeve. NIGERIA : Agberi (R. Niger), Boma, Ilesha. SUDAN : Tembura, White Nile (Lat. 12° 11′N).

S. botanephaga is a rather variable species, as regards both coloration and details of the male genitalia. The most noteworthy of the colour variants are :—

(1) A very pale form, almost white in ground colour and with correspondingly pale wing markings, most frequently obtained towards the end of the rains or during the dry season.

(2) A very dark form with considerable fuscous-black or fuscous irroration, prevalent at the beginning of the rains.

Adults emerging during the greater part of the wet season are more uniformly buff or cartridge buff with more pronounced wing markings.

The variation found in the male genitalia largely concerns the costal spine (fig. 13). There is some indication that specimens from the dryer parts of the insect's range, at least in the Gold Coast, have a more heavily toothed costal spine and generally larger and stouter genitalia.

This species has previously been treated in West Africa as *S. calamistis*. It differs from the latter mainly in the form of the male and female genitalia, but for most of West Africa the two species are readily separated by superficial characters, *botanephaga* being larger, generally lighter in colour and more definitely marked on the wings. The ecological requirements of the two species are also different, *botanephaga* being dominant in forest and fringing-forest areas where there is a minimum rainfall of about 50 ins. well distributed through the year and therefore a relatively short and less severe dry season. *S. calamistis*, on the other hand, is commoner, at least in West Africa, in savannah areas which have a well marked dry season.

S. botanephaga is undoubtedly a most serious pest of maize within its area of dominance. In the Gold Coast, infestations in some districts may reach 100 per cent. and cause almost complete loss of crop, especially in the late (September) planted maize ; indeed, in many cases native farmers are reluctant to plant this late crop because of borer damage. In addition to maize, *S. botanephaga* has been reared from Guinea corn (*Sorghum vulgare*), rice, sugar-cane and several grasses, the most important of which are *Pennisetum purpureum*, *Sorghum arundicaceum*, *Rottboellia exaltata*, *Chasmopodium afzelii* and *Setaria* ? *chevalieri*.

Sesamia madagascariensis Saalmüller.

Sesamia madagascariensis Saalmüller 1891, Lep. Madagascar, p. 262.

♂. Palpus pale buff-white, considerably infuscate. Antenna strongly bipectinate, cilia short, fasciculate. Head cartridge-buff to ochraceous-buff, slightly infuscate. Thorax anteriorly cartridge-buff to ochraceous, sparsely streaked with fuscous, posteriorly more cartridge-buff without fuscous markings. Pectus infuscate. Legs buff, fore tibia infuscate. Forewing ochraceous-brown with variable fuscous-brown suffusion ; some fuscous to fuscous-black markings varying in extent and intensity ; an antemedial fuscous patch below the cell ; a small fuscous patch about middle of discocellulars ; an indefinite curved postmedial fascia of one row of fuscous to fuscous-black spots on the veins ; a fine fuscous terminal line ; the whole wing surface with fuscous irroration of variable intensity ; fringe greyish white tipped with fuscous. Hindwing with variable pale buff to pale fuscous suffusion along costa, termen and inner margin. Underside of forewing fuscous-brown, more ochraceous-buff along costa and with variable fuscous irroration ; a fuscous patch at middle of discocellulars and a fine fuscous terminal line. Underside of hindwing white with pale buff to pale ochraceous-buff suffusion along costa, termen and inner margin and some fuscous irroration along costa and termen.

Expanse, 31–34 mm.

Male genitalia rather similar to those of *S. botanephaga*. Tegumen with moderate peniculus. Uncus hook-shaped, gradually tapering to a point. Valve (figs. 15, 16) with sacculus and cucullus separate ; costal spine long, curved inwards, simple ; apical extension of sacculus with a crest of several rows of short stout spines, its inner margin extended almost to costal margin ; cucullus slightly clavate at apex. Aedoeagus very short, manica produced ventrally into paired, lateral, minutely scobinate lobes, more strongly scobinate dorsally ; vesica broadly sclerotised dorsally at base, with a weak, slightly ridged mid-ventral cornutus. Juxta (fig. 17) conical, the base produced into a blunt point. Vinculum with a broad, shallow, ventral expansion.

Female similar to male, but sometimes with considerably more extensive fuscous markings, including a longitudinal fuscous fascia along the lower margin of the cell, partly within and partly without the cell, extending to the termen which may have a broad fuscous suffusion and a well marked terminal line. Expanse, 34–38 mm. Female genitalia very similar to those of *S. calamistis* and *S. nonagrioides*, but with the anteostial pad very small, not as wide as the ostium.

MADAGASCAR : Nanisan, near Antananarivo ; Mananjary.

The original description of Saalmüller's species applies equally well to the present species and *S. calamistis*, which also occurs in Madagascar. Without an examination of the types, it is not possible to say which species Saalmüller had before him, but the name *madagascariensis* is here retained for a distinct species apparently restricted to Madagascar. In the male it differs from *calamistis* in the shape of the costal spine, which is pointed and curved inwards, the stouter extension of the sacculus, the midventral situation of the cornutus and the conical juxta ; in the female, practically the only difference lies in the extremely small anteostial pad of *madagascariensis*.

Biology unknown.

Sesamia calamistis Hampson (figs. 65, 70, 71).

Sesamia calamistis Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 325, pl. CXLIV, fig. 18.

Sesamia vuteria Stoll, Hampson (*ex errore*) 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 324, text fig. 142, ♂—nec Stoll (pl. O, fig. 11 is a copy of fig. 142 (*ex parte*)).

Sesamia mediastriga Bethune-Baker 1911, Ann. Mag. nat. Hist., (8) **8**, p. 518. (*syn. nov.*).

♂. Palpus largely infuscate. Antenna (fig. 51) moderately bipectinate, serrate at apex, cilia short, fasciculate. Head light ochraceous-buff, streaked with fuscous-brown. Thorax buff or light buff, variably suffused with ochraceous. Pectus buff, infuscate at base. Legs light buff, sometimes with ochraceous suffusion, the fore femur and tibia moderately, the mid and hind tibiae lightly, streaked with fuscous. Forewing light cartridge-buff, variably irrorate with fuscous and suffused with fuscous along termen ; some fuscous to fuscous-black markings variable in extent and intensity ; a longitudinal fuscous to fuscous-black fascia from base along lower margin of cell, partly within cell, partly without, extending to termen ; a fuscous-black spot at apex of cell, a slightly dentate fuscous-black postmedial fascia, the point between veins 5 and 6 frequently prominent, sometimes separated into two rows of fuscous-black spots, the proximal row on the veins, the distal interneural, a narrow fuscous-black terminal line ; fringe ochraceous-white, lightly infuscate at middle and tip. Hindwing white. Underside of forewing white, costa suffused with light buff, costa and termen irrorate with fuscous ; a fuscous-black spot at apex of cell. Underside of hindwing white.

Expanse, 22–30 mm.

Male genitalia (figs. 47, 72). Tegumen with well developed peniculi. Uncus small, narrow. Valve (figs. 18, 19) with sacculus and cucullus separate ; costal spine (fig. 20) short, straight, with a small tooth immediately before apex, sometimes almost bifid sometimes without apical tooth ; extension of sacculus narrow, slightly curved inwards with several rows of short stout spines which may extend almost to costal spine ; cucullus long, slightly spatulate at apex. Aedoeagus short, dilated basally ; manica scobinate dorsally, lateral lobes elongate, scobinate ; vesica with apical flat cornutus. Juxta (fig. 21) broad trapezoid. Vinculum with fairly deep ventral expansion.

Female similar to male ; expanse, 24–36 mm. Genitalia (fig. 48) with bursa copulatrix short and rounded, ductus bursae short and broad, ostium broad, the anteostial pad as long or nearly as long as ostium, lateral plates of ostial segment reduced and lightly sclerotised.

SOUTH AFRICA : Cape Colony ; Grahamstown, Transkei ; Zululand, Eshowe ; Natal, " Coast ", Durban ; Bura, Zimbile ; Barberton ; Pondoland ; Pt. St. John. NORTHERN RHODESIA : Gimson. NYASALAND : Zomba. UGANDA : Kampala. TANGANYIKA : Amani, " Ent. Lab " ; Songea 3,800 ft. KENYA : Meru District. ZANZIBAR. MADAGASCAR : Diego Suarez ; Perinet ; Mananjary ; Nasisana, near Antananarivo ; Grand Comoré. MAURITIUS : Réduit. RÉUNION. ANGOLA : Pungo Adongo ; Quirimbo, 75 km. east of P. Amboim, 300 m. CAMEROONS. NIGERIA : Warri ; Anambara Creek, Niger ; Ogruga, Niger ; Ibadan. GOLD COAST : Gold Coast Colony, Kpeve, nr. Accra ; Pokoase ; Aburi ; Dawa ; Somanya ; Ashanti ; Kumasi. IVORY COAST : Bingerville. SENEGAL : Sédhiou : Kaolack. GAMBIA.

S. calamistis is a widely distributed and very variable species. Although Hampson's type specimens came from the southern limit of distribution—Cape Province—the most uniform and " typical " examples of the large number examined are from East and Central Africa, the central area of the range of the species. Compared with these central specimens, there are two major variants, the divergences of which become more pronounced with increasing geographical separation from East and Central Africa. These variations consist of :—

(1) A great reduction in the fuscous-black wing markings, especially in southern and western forms, often combined in extreme western localities (Gambia) with a pronounced yellowish tinge or (Gold Coast) a strong ochraceous suffusion.

(2) A reduction in size, particularly noticeable in specimens from western areas (Gambia, Gold Coast, and to a less extent, Nigeria) and also Mauritius and Réunion.

The melanism noted in early wet season adults of *S. botanephaga* also occurs in such adults of *S. calamistis*, at any rate in the Gold Coast.

In addition to colour variations, there are considerable differences in the shape of the costal spine in the male genitalia (fig. 20) ; these differences also show some geographical correlation. In typical *calamistis*, the costal spine is short, more or less straight and with a pronounced sub-apical tooth ; a common form from the east coast of Africa and from Mauritius has the sub-apical tooth obsolete, and Angolan specimens are intermediate with a reduced sub-apical tooth. West African examples may show either of these characters combined with a general reduction in size of the genitalia.

In spite of any apparent geographical restriction of these various forms, it is difficult to give subspecific status to any one of them. Although Gold Coast *calamistis*, for example, are distinct from East African *calamistis*, it is nevertheless possible to find a graded series connecting both forms ; similarly with the southern and eastern " races ".

The economic status of *Sesamia calamistis* has been obscured by previous references to it as "*Sesamia vuteria* Stoll". It is a major pest of sugar-cane in Mauritius, where its biology has been worked out by d'Emmerez de Charmoy (1916, 1921) and Moutia (1932, 1934) under the name "*vuteria*". Ritchie (1927) records it, as *calamistis*, from rice and maize in Tanganyika, and Seydel (1929) refers to it in the Belgian Congo. West African records are few. Golding (1946) lists it among Nigerian pests, although it has been confused in the past in Nigeria with *S. botanephaga* ; in the Gold Coast, *calamistis* is less important than *botanephaga*, infestations attributable to the former species rarely rising above 20 per cent., and the record of Cotterell (1925) almost certainly refers mainly to *botanephaga*.

In addition to the cultivated food-plants listed above, *S. calamistis* has been reared in the Gold Coast from *Pennisetum purpureum* and *Sorghum arundinaceum*.

Sesamia jansei, sp. n.

Sesamia calamistis Hampson, Janse 1940 (nec Hampson), Moths S. Africa, **3,** p. 367, text fig. 91, Pl. XXI fig. 8, Pl. XXXI fig. 17.

♂. Palpus pale cartridge-buff, suffused with fuscous-buff and irrorate with fuscous. Antenna (fig. 52) bipectinate, cilia short, fasciculate. Head buff, suffused ochraceous and sparsely streaked with fuscous. Thorax cartridge-buff, anteriorly suffused with ochraceous-buff and sparsely streaked with fuscous. Pectus fuscous. Legs cartridge-buff, fore tibia infuscate, middle tarsus ochraceous. Forewings pale buff with pale fuscous-buff suffusion towards apex and on termen ; cubital vein and veins 3, 4, 5, and 6 distinctly white, radius and veins 1, 7 and 8 more buff-white ; some fuscous to fuscous-black markings ; an antemedial fuscous-black patch below the cell ; indistinct longitudinal fuscous-buff fascia along lower margin of cell, partly within the cell and partly without, and extending just beyond apex of cell ; a curved postmedial fascia of fuscous spots which are on the veins and a more proximal curved fuscous line connecting the spots on veins 5 and 6 ; a fine fuscous terminal line of uniform width but interrupted at the apices of veins 2–4 ; the whole surface fuscous irrorate ; fringe infuscate. Hindwing entirely white. Underside of forewing white, suffused buff on costa and termen, irrorate fuscous at apex and on termen, veins fuscous towards termen. Underside of hindwing white, costa suffused buff and irrorate fuscous.

Expanse, 30 mm.

Genitalia (fig. 49) : tegumen with large peniculus. Uncus hook-shaped with small hook at apex. Valve (fig. 22) with sacculus and cucullus separate ; costa narrowly sclerotised, costal spine (fig. 23) long, curved, dentate ; extension of sacculus broad, bearing several very large spines along its inner margin, the spines extending almost to costa ; cucullus broad with flattened apex. Aedoeagus short, stout ; manica with irregular, rather small spines ; vesica lightly sclerotised at base with a semi-circular cornutus at apex. Juxta (fig. 24) small, rather trapezoidal. Vinculum narrowly expanded ventrally with very small saccus.

Female similar to male, slightly larger. Expanse, 32–45 mm. Genitalia (fig. 50) very similar to *S. botanephaga*, but lateral plates of ostial segment narrower and the ostial pad much smaller, distinctly indented along the posterior margin.

South Africa : Pretoria ; Natal, Durban.

Sesamia coniota Hampson.

Sesamia coniota Hampson 1902, Ann. S. Afr. Mus., **2,** p. 297.

Sesamia coniota Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 329.

♂. Palpus white suffused with light buff, infuscate. Antenna shortly bipectinate. Head white suffused with light buff or light ochraceous. Thorax light buff, suffused with light ochraceous anteriorly. Pectus light buff, lightly infuscate at base. Legs light buff, fore tibia and apices of tarsi infuscate. Abdomen white suffused with light buff. Forewing light buff suffused with light ochraceous and sparsely irrorate with fuscous ; some fuscous to fuscous-black markings ; a fuscous-black antemedial spot ; an indistinct fuscous spot at apex of cell ; a curved postmedial fascia of one row of fuscous-black spots on the veins ; a terminal series of black points between the veins ; fringe white. Hindwing white. Underside of forewing white, suffused with light ochraceous along costa and sparsely irrorate with fuscous at apex. Hindwing white.

Expanse, 18–24 mm.

Male genitalia very similar to those of *jansei*, but apical extension of sacculus much broader, costal spine smaller and stouter. Aedoeagus narrower, manica more heavily spinose. Juxta larger, shovel shaped.

Female not known.

Southern Rhodesia : Mashonaland, Salisbury.

This small species is very close to *jansei*, but is easily separable from it by the very shortly bipectinate antennae.

Biology unknown.

Sesamia epunctifera Hampson.

Sesamia epunctifera Hampson 1902, Ann. S. Afr. Mus., **2,** p. 298.

Sesamia epunctifera Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9,** p. 329.

♂. Palpus white with cartridge-buff and fuscous irroration. Antenna serrate, cilia short or very short, fasciculate. Head cartridge-buff to white with pale buff suffusion, streaked with fuscous. Thorax varying from pale cartridge-buff with ochraceous-buff suffusion anteriorly streaked with fuscous to white with pale buff suffusion streaked with fuscous. Pectus grey-white with buff suffusion and centrally infuscate, to completely infuscate. Legs buff to white with pale buff suffusion, fore tibia lightly to fairly heavily streaked with fuscous. Forewing pale cartridge-buff, sometimes almost white with pale buff suffusion and sometimes a pale fuscous suffusion along termen ; some fuscous to fuscous-black markings ; an antemedial patch below cell ; a curved postmedial fascia of fuscous-black spots consisting of one row on the veins ; a terminal fascia of interneural fuscous-black spots ; fuscous irroration scattered over the whole surface ; fringe infuscate. Hindwing white with very light fuscous suffusion along the costa, termen and inner margin, with scattered fuscous irroration ; veins sometimes with small light fuscous patches ; terminal line light to dark fuscous ; fringe infuscate at base. Underside of forewing very pale buff, more cartridge-buff along costa with light fuscous suffusion along termen ; some fuscous irroration along costa and termen ; a terminal fascia of interneural fuscous-black spots. Underside of hindwing white with pale buff suffusion along costa which is also irrorate with fuscous ; an indistinct light fuscous terminal line sometimes slightly widened interneurally.

Expanse, 22–27 mm.

Male genitalia : tegumen with rather squat peniculus. Uncus small, tapering to a point. Valve (figs. 25, 26) with sacculus, and cucullus separate ; costal spine short and thick, apex bifid ; apical extension of sacculus club-shaped with several rows of short stout spines ; cucullus narrow, somewhat broadened at apex. Aedoeagus short, slender ; manica scobinate, produced ventrally into paired lateral scobinate lobes ; vesica with flattened apical cornutus. Juxta (fig. 27) broadly conical, produced apically into a blunt point. Vinculum with ventral expansion large, indented.

Female not known.

South Africa : Cape Province ; Annshaw.

Together with the three following species, *S. epunctifera* constitutes a distinct group within the *nonagrioides* section, characterised in the male by the shortly bipectinate or serrate antennae, and by the short, stout recurved costal spine on the valve. In the female, of which only two specimens are definitely known, the ostial segments bears large, heavily sclerotised, lateral plates which are triangular or sub-triangular in shape, approximate medially and extend well beyond the ostial opening.

Sesamia epunctifera is an East and South African species, and as with most of the species in this genus, geographical variation occurs. Northern specimens appear distinctly grey because of the heavy fuscous irroration of the wings and thorax, while southern examples, with considerably less fuscous irroration, appear much more buff.

Biology unknown.

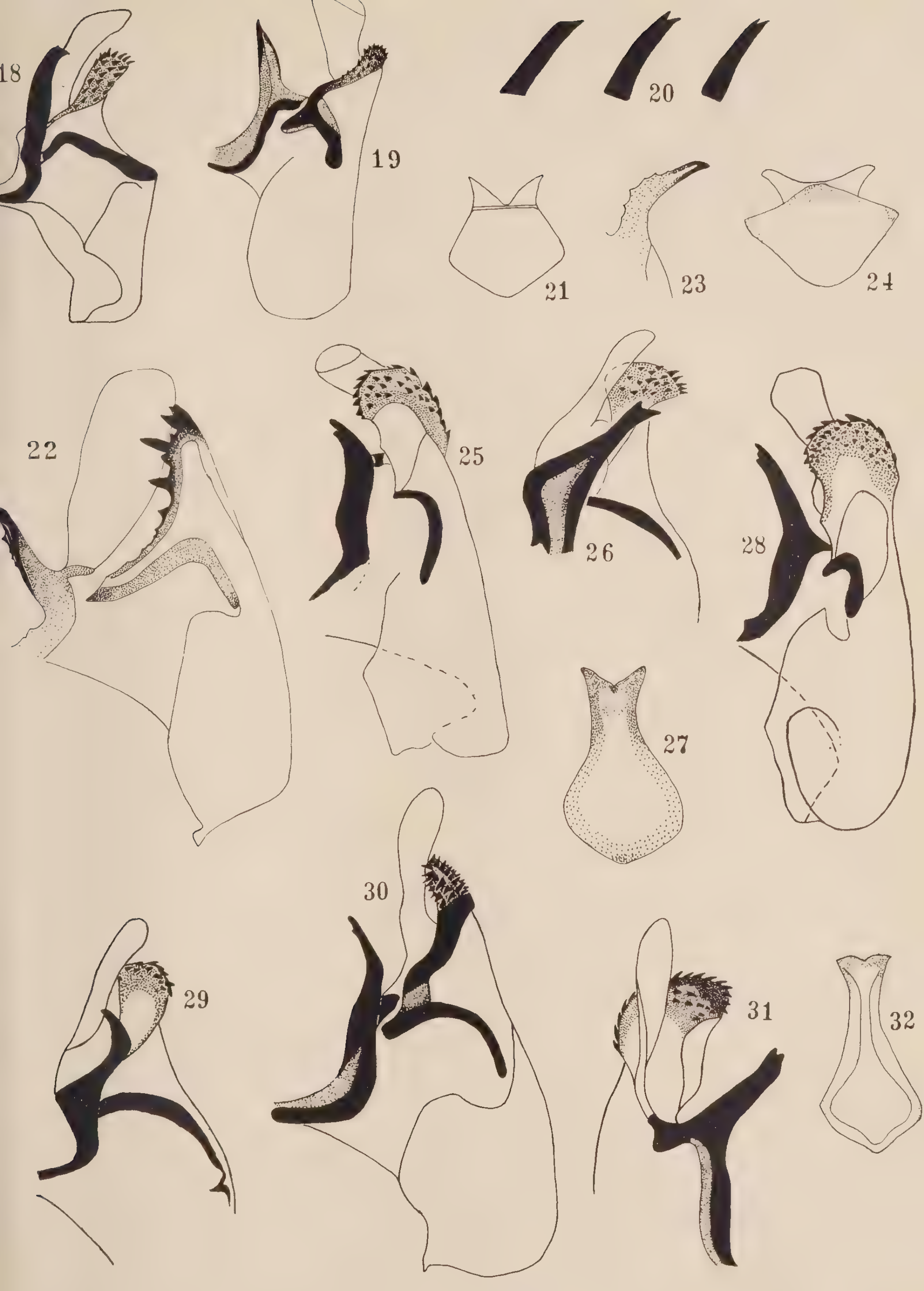
Sesamia poephaga, sp. n.

♂. Palpus light cartridge-buff, lightly infuscate. Antenna shortly bipectinate, cilia short, fasciculate. Head light cartridge-buff, lightly streaked with fuscous but infuscate above palpus. Thorax light cartridge-buff, almost white posteriorly, suffused with ochraceous and lightly streaked with fuscous anteriorly. Pectus white with pale buff suffusion, medially infuscate. Legs white with pale buff suffusion, not or very slightly infuscate. Forewing cartridge-buff, veins outlined with white ; some fuscous-brown to fuscous-black markings, variable in extent and intensity ; an antemedial fuscous-black patch below cell ; a longitudinal fuscous fascia along the lower margin of the cell, partly within the cell partly without, extending to discocellulars ; a curved postmedial fuscous fascia of one row of spots on the veins with a single more proximal spot between veins 5 and 6 ; a narrow terminal fuscous line which may be very indistinct ; some fuscous irroration particularly along the costa and dorsum ; fringe white suffused with light buff at tips. Hindwing white. Underside of forewing pale cartridge-buff irrorate with fuscous, with a fuscous smudge along lower margin of cell largely within the cell. Underside of hindwing white, base of costa faintly suffused with pinkish buff, apex irrorate with fuscous.

Expanse, 26–30 mm.

The male genitalia differ from those of *epunctifera* in that the apical extension of the sacculus is much broader, the lateral lobes of the manica larger, the juxta larger and more rounded, and the ventral expansion of the vinculum not indented.

Female similar to male, but colour varying from cartridge-buff with ochraceous suffusion to almost rufous, with the postmedial fascia in the latter case well marked and often in two connected rows ; expanse, 29–38 mm. Female genitalia with



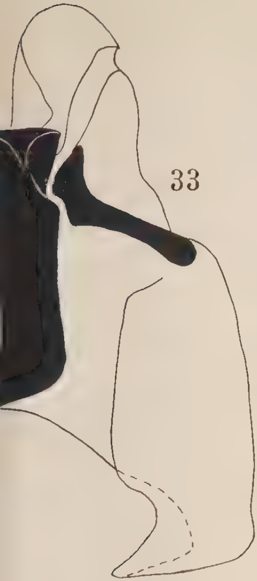
Sesamia calamistis Hampson. Fig. 18, valve, ventral view; Fig. 19, valve, latero-ventral view; Fig. 20, variation in costal spine of valve; Fig. 21, juxta, ventral view.

Sesamia jansei, sp.n. Fig. 22, valve, ventral view; Fig. 23, costal spine, lateral view; Fig. 24, juxta, ventral view.

Sesamia epunctifera Hampson. Fig. 25, valve, ventro-lateral view; Fig. 26, valve, internal view; Fig. 27, juxta, ventral view.

Sesamia penniseti, sp.n. Fig. 28, valve, ventral view; Fig. 29, valve, internal view.

Sesamia poebora, sp.n. Fig. 30, valve, ventral view; Fig. 31, valve, internal view; Fig. 32, juxta, ventral view.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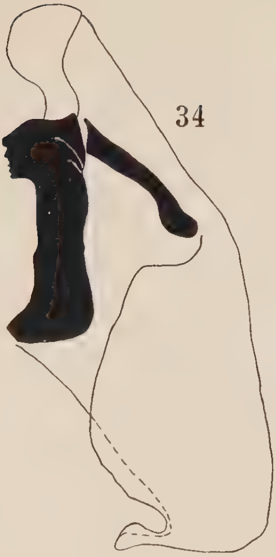
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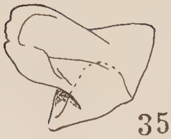
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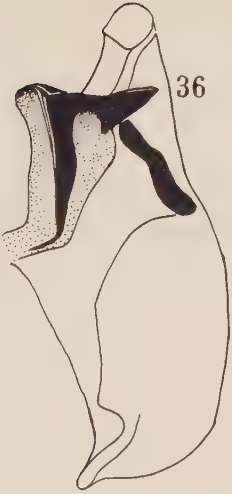
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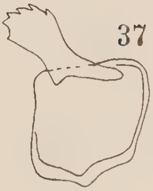
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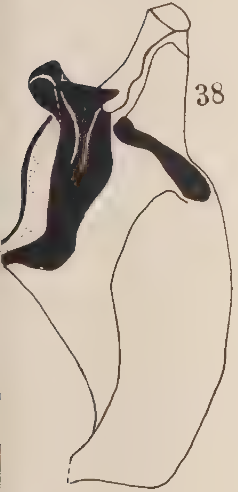
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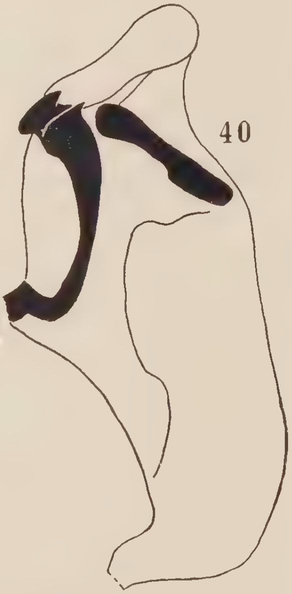
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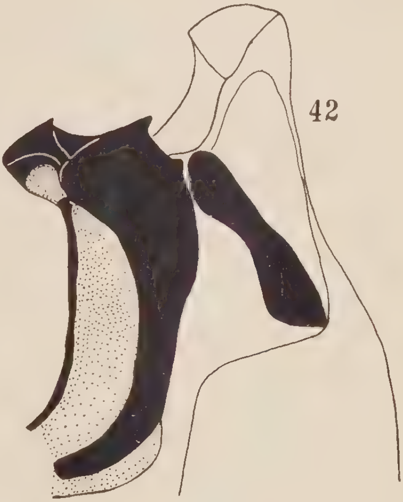
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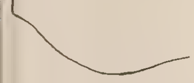
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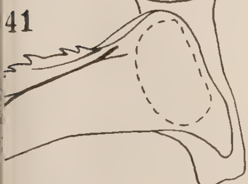
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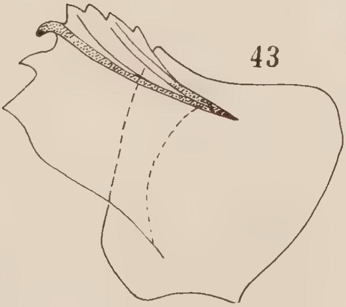
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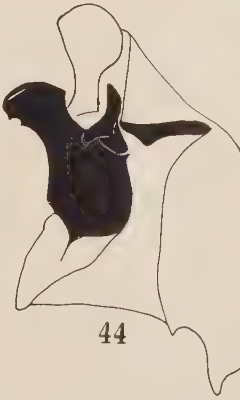
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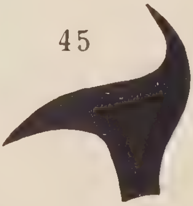
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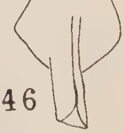
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Sesamia cretica Lederer. FIG. 33, valve, ventral view; FIG. 34, valve, lateral view; FIG. 35, juxta, latero-ventral view.

Sesamia taenioleuca (Wallengren). FIG. 36, valve, ventral view; FIG. 37, juxta, ventral view.

Sesamia albivena albivena Hampson. FIG. 38, valve, ventral view; FIG. 39, medial process of juxta.

Sesamia albivena sudanensis, subsp.n. FIG. 40, valve, ventral view; FIG. 41, juxta, lateral view.

Sesamia albivena mocoënsis, subsp.n. FIG. 42, apex of valve, ventral view; FIG. 43, juxta, lateral view.

Sesamia rufescens Hampson. FIG. 44, valve, ventral view; FIG. 45, clasper, lateral view; FIG. 46, juxta, ventral view.

bursa copulatrix moderately large ; ductus bursae strongly sclerotised at base. Anteostial pad large, broad and rounded posteriorly. Lateral plates of ostial segment large, heavily sclerotised, medially approximate, and produced towards margin of ostial segment. Ovipositor lobes relatively long and narrow.

Type ♂ : GOLD COAST : Northern Territories, Ketekrachi. 1926 (*A. W. Cardinall*).

Allotype ♀ : TANGANYIKA : Chunya District, Chunya, 2650ft., 1947 (*G. Swynnerton*).

Paratypes : MADAGASCAR : ♀ Comoro Is. SOUTHERN RHODESIA : ♀, Mashonaland, Salisbury, 12.ii.1898 (*G. A. K. Marshall*) ; 2♀♀, Zambesi, Caia, 29.viii.1929 (*G. A. K. Marshall*). NYASALAND : ♀, West shore L. Nyasa, Domira Bay, 26.x.1912 (*S. A. Neave*). KENYA : ♂, Nairobi, 30.iv.1905 (*F. J. Jackson*) ; ♀, Moa, 30 miles N. of Tanga, Sea Coast, –.v.1923 (*W. Feather*). UGANDA : ♀ Masindi. SOUTH SUDAN : ♀, Tembura, –.xii.1922. NIGERIA : 2♀♀, Anambara Creek, Niger ; ♀, Ogruga, R. Niger. GOLD COAST : ♀, North Ashanti, Wenchi, 7.xii.1947 (*ex* maize) ; 5♀♀, British Mandated Togoland, Kpeve, –.x.1949 (*ex* maize). IVORY COAST : ♀, Bingerville, 1–5.viii.1918.

This rather large and heavily built species belongs to the *epunctifera* group. It is extremely similar to the next species, *penniseti*, and indeed further investigation may show them to be races of one widely distributed species. In the Gold Coast, however, the distribution of *poephaga* and *penniseti* is notably different, a difference which parallels that of *botanephaga* and *calamistis*. *S. poephaga* occurs in the southern reaches of the savannah zone, south of the R. Volta, and in the transition zone of Southern Togoland, whereas *S. penniseti* has only been found in the forest area. *S. poephaga*, although frequently found boring in stems of maize, is of less importance in the areas in which it occurs than *Busseola fusca* and the Pyralid, *Eldana saccharina* Walker. It has been obtained from maize only.

Sesamia penniseti, sp. n.

♂. Palpus fuscous, streaked white or pale cartridge-buff. Antenna shortly-bipectinate, cilia short, fasciculate. Head pale cartridge-buff, fairly heavily streaked with fuscous. Thorax cartridge-buff to more distinctly buff, much streaked with fuscous, particularly anteriorly, the thorax thus appearing rather fuscous-buff. Pectus fuscous-buff to buff-white, infuscate at apex, fuscous medially. Legs pale cartridge-buff to buff-white, variably irrorate with fuscous, fore femur infuscate. Abdomen cartridge-buff, white laterally at base, suffused and irrorate with fuscous-buff, anal tuft cartridge-buff streaked with fuscous. Venter more ochraceous-buff, streaked with fuscous-buff. Forewing cartridge-buff with considerable ochraceous-buff, fuscous-buff or rather pale fuscous suffusion ; some fuscous to fuscous-black markings varying in extent and intensity ; an antemedial fuscous-black spot below the cell ; a longitudinal fuscous fascia, almost a smudge, along lower margin of cell, rather narrow along this margin, partly within the cell and partly without, extending through the cell, where it broadens, to the discocellulars or even to the termen ; a postmedial curved fascia of two rows of fuscous-black spots, the proximal row of two to three spots at the discocellulars, the distal row more extended, and on the veins the lower spots of the distal row connecting with the corresponding spots of the proximal row, thus producing a scalloped effect ; a fuscous-black terminal line ; variable fuscous-black irroration ; fringe basally buff-white, infuscate at tips. Hindwing white, lightly irrorate with fuscous at apex, with a fine fuscous terminal line ; fringe infuscate at apex. Underside of forewing white suffused with buff, and irrorate with fuscous along costa, with a fairly heavy fuscous suffusion from base of cell to termen, more confined to veins near the termen ; a terminal fascia of interneural fuscous-black spots. Underside of hindwing white, suffused with buff and irrorate with fuscous along costa ; fringe infuscate, particularly at apex.

Expanse, 28–30 mm.

Genitalia similar to *epunctifera*. Tegumen with more prominent peniculus. Costal spine of valve (figs. 28, 29) bent outwards, with a single, recurved apical hook ; extension of sacculus very broad and heavily spinose. Ventral edge of vinculum curved outwards, not indented.

Female similar to male, but forewings frequently distinctly brownish-buff with the fuscous markings reduced or obsolete ; expanse, 28–37 mm. Genitalia very similar to *poephaga*, but bursa copulatrix smaller, ductus bursae less heavily sclerotised ; anteostial pad more conical ; plates of ostial segment more rounded—quadrate, and ovipositor lobes relatively shorter and broader.

Type ♂ : GOLD COAST : Ashanti, Owabi, 29.ii.1950, ex *Pennisetum purpureum*.

Allotype ♀ : GOLD COAST : Ashanti, Kumasi, 11.iv.1950, ex *Pennisetum purpureum*.

Paratypes : GOLD COAST : Ashanti ; ♀, Kumasi, 18.ii.1950 ; ♂, Kumasi, 30.vi.1950 ; ♂, Kumasi, 4.vii.1950 ; ♀, Owabi, 22.iii.1950 ; 2♀♀, Owabi, 13.iii.1950. All ex *Pennisetum purpureum*.

This species is extremely close to *S. poephaga*. Apart from details of the genitalia, the two species can be conveniently separated by the form of veins 6 and 7, which are sessile in *penniseti* and stalked in *poephaga*.

S. penniseti exhibits more sexual dimorphism than any other species of the genus, the females almost invariably being much lighter in colour and with less conspicuous fuscous wing markings.

The species has so far been found only in localities in wet forest zones. In the two Gold Coast localities, it is frequent and sometimes common in *Pennisetum purpureum* ; at Owabi, it is the dominant species in this grass. *S. penniseti* has been reared occasionally from maize, but is of no economic importance.

Sesamia poebora, sp. n.

♂. Palpus pale cartridge-buff, infuscate. Antenna shortly bipectinate, cilia short, fasciculate. Head pale cartridge-buff, streaked with fuscous. Thorax pale cartridge-buff, anteriorly streaked with fuscous. Pectus pale cartridge-buff, infuscate basally. Legs pale cartridge-buff, fore femur infuscate, fore tibia streaked with fuscous. Abdomen white suffused with pale buff, anal tuft white suffused with pale fuscous and lightly streaked with fuscous. Forewing light yellowish-buff, suffused with light fuscous-buff at apex and along termen ; some fuscous to fuscous-black markings ; an indistinct fuscous-black patch along upper margin of cell and within it ; an indistinct fuscous-black patch along lower margin of cell and within it ; a medial fuscous-black patch below cell ; a curved postmedial fascia of fuscous-black spots consisting of two rows, the proximal row interneural, the distal on the veins, both rows connected, thus producing a scalloped effect, the spot on the second vein connected to the medial patch below the cell, the spot on the first vein isolated ; a fuscous-black terminal line interrupted at the veins ; some scattered fuscous irroration, particularly at the base ; fringe lightly infuscate. Hindwing white. Underside of forewing cartridge-buff, with a broad medial pale fuscous suffusion which extends above and below the cell ; some pale fuscous irroration. Underside of hindwing white, suffused with buff and irrorate with fuscous along costa.

Expanse, 30 mm.

Genitalia very similar to *epunctifera*, but costal spine of valve (figs. 30, 31) much stouter and more bifid at apex, apical extension of sacculus much broader and more heavily spinose, cucullus broader, and juxta (fig. 32) more narrowly conical with a sharper apical point.

Female not known.

UGANDA : Kawanda, 8.x.1940, ex *Pennisetum purpureum* (*T. H. C. Taylor*) (type ♂).

A very distinct species of the *epunctifera* group, separable from all the other species by the characteristic wing markings, consisting of three median fuscous patches and a strongly dentate post-medial fascia.

The occurrence of this East African species in *Pennisetum purpureum* is of interest, since the usual food-plant of the West African *penniseti* is also *P. purpureum*.

A female from South Africa (Okahandja) is doubtfully referred to this species. It is similar in wing colour to the male described above, but with less extensive fuscous wing markings, which consist of an indistinct longitudinal fuscous fascia, and a fuscous terminal line interrupted at the vein endings. The genitalia are of the *poephaga-penniseti* type, but the plates of the ostial segment are triangular and very small, much less strongly developed than in either of the other species.

Sesamia cretica Lederer.

Sesamia cretica Lederer 1857, Noct. Eur., p. 225.

Sesamia cretica Lederer, Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 333.

Sesamia vuteria vuterioides Strand 1915, Arch. Naturgesch., **80**, A10, p. 101 (not *vuteria* Stoll).

Sesamia cretica rufescens Schawerda 1916, Verh. zool.-bot. Ges. Wien, **66**, p. 239 (preoccupied by *rufescens* Hampson 1910).

Sesamia vuteria Stoll, Mariani 1934 (nec Stoll), Boll. Soc. ent. ital , **66**, pp. 184–188.

Sesamia pecki Tams 1938, Bull. ent. Res., **29**, p. 9, pl. 1, figs. 1–3 (*syn. nov.*). [illegible]

♂. Palpus cartridge-buff or pale cartridge-buff, sometimes irrorate with fuscous. Antenna serrate, cilia short, fasciculate. Head buff to very pale buff, frons sometimes infuscate. Thorax buff to very pale buff with a buff suffusion anteriorly in pale specimens. Pectus buff to cartridge. Legs buff or cartridge-buff with the fore tibia sometimes infuscate. Forewing ochraceous-buff to very pale buff, with some fuscous to fuscous-black markings, varying in extent and intensity ; a sub-basal patch below the cell, followed by a similar but smaller antemedial spot ; a longitudinal fuscous fascia along the lower margin of the cell, partly within the cell, partly without, extending beyond end of cell to postmedial series of spots or sometimes to termen ; a prominent fuscous-black spot at lower angle of cell, a smaller one above it at middle of discocellulars ; a curved postmedial fascia of fuscous-black spots, consisting of two rows, the proximal row interneural, the distal on the veins ; a fine fuscous-black terminal line, slightly widened interneurally ; fringe irrorate with fuscous. Hindwing white, termen and inner margin tinged with cartridge-buff. Underside cartridge-buff to light ochraceous-buff, forewing tinged sometimes with ochraceous-buff, hindwing with very pale buff suffusion along costa and termen.

Expanse, 26–32 mm.

Male genitalia : tegumen with very small peniculi. Uncus curved, simple. Valve (figs. 33, 34) with cucullus and sacculus fused ; costal margin broadly sclerotised costal spine broad, rather triangular at apex ; sacculus with an oblique sclerotised bar at apex ; cucullus broadly rounded. Aedoeagus short and slender ; manica strongly spinose. Juxta (fig. 35) with a small, laterally compressed, medial projection, rounded at apex. Vinculum with ventral expansion indented on lower margin.

Female similar to male ; expanse, 29–40 mm. Genitalia with bursa copulatrix short and broad, rather pointed at apex, ductus bursae very short. Anteostial pad moderately large, almost quadrate. Ostium strongly transverse, the anterior lip sclerotised. Ostial segment with a lightly sclerotised band immediately posterior to ostium.

ITALY : Villa Latina. CORSICA. YUGOSLAVIA : Dalmatia. CRETE. MOROCCO : Oran. EGYPT : Aswan. SUDAN. ABYSSINIA : Dire Daoua. BRITISH SOMALILAND : Burao. SYRIA. ARABIA : Jiddah ; South Hejaz ; Taif.

The rather sharp differences of structure between the *nonagrioides* and *cretica* sections of *Sesamia* have been referred to earlier. There is, however, insufficient reason to separate them into distinct genera, the two sections having many features in common, quite apart from the fact that species such as *S. jansei* and *S. coniota* are natural links.

Sesamia cretica is widely distributed throughout the Middle East, North and north-east Africa and Mediterranean Europe except France and the Iberian peninsula where it is replaced by *S. nonagrioides*. Like other widely distributed species of *Sesamia*, *S. cretica* is very variable, this variation being most apparent at the extremes of its range. If one assumes the Middle East and north-east Africa (Syria, Egypt, the Anglo-Egyptian Sudan) to be its centre, an assumption supported by the uniformity of specimens from these areas, there are three main local races :—

(1) An ochraceous to ochraceous-buff form from the Balkan area (*S. cretica rufescens* of Schawerda was described from Bosnia).

(2) A very pale yellowish-buff form from Morocco and the south-western Mediterranean.

(3) A light cartridge-buff form with well defined fuscous markings from S. Arabia, British Somaliland and Ethiopia. It is probable that specimens of *cretica* from Italian Somaliland belong to this type, which was described as *S. pecki* Tams.

S. cretica is a major pest of sorghum, and to a less extent maize, wherever it occurs. It has also been recorded from bullrush millet (*Pennisetum typhoideum*) (Bedford, 1936), and *Sorghum halepense*. What is probably this species is recorded by Balachowsky and Mesnil (1936) as occurring in bamboo and even young palms in North Africa, and also in *Saccharum spontaneum*.

The most detailed account of the morphology of all stages of this insect is that of Cuscianna (1935), who also gives an account of its depredations in Venezia Giulia. Hergula (1930) refers to it in Yugoslavia. There are several references to it in the Sudan (Bedford, 1936, 1938, 1940 ; Cowland, 1930), and Chiaromonte (1948) gives a summary of the position in Italian Somaliland.

Sesamia taenioleuca (Wallengren).

Tapinostola taenioleuca Wallengren 1866, K. svensk. VetensAkad. Handl., **4**, p. 58.

Sesamia taenioleuca Wallengren, Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 330, pl. CXLIV, fig. 23.

♂. Palpus light buff, infuscate. Antenna serrate, cilia short. Head white suffused with pale buff. Thorax white suffused with buff on anterior margin and strongly suffused with purplish-pink on tegulae and lateral margins. Pectus infuscate. Legs white, with pale pinkish-buff suffusion at apex of femora, tibiae suffused with salmon-pink. Abdomen pale buff suffused with pink. Forewing purplish-pink ; costa white, a longitudinal white fascia from base of cell running through middle of cell to just before termen, a second longitudinal white fascia from base running below cell to just before termen ; fringe fuscous with narrow white basal line and tinged with pink at tips. Hindwing white suffused with pinkish at apex and termen, fringe pink at tips. Underside of forewing white, costa and apex suffused with purplish-pink, the median area pale fuscous. Underside of hindwing white, costa and termen suffused with pink.

Expanse, 42 mm.

The male genitalia differ from those of the following species, *S. albivena*, in that the costal spine of the valve (fig. 36) is produced inwardly into a large triangular process, the projection of the juxta (fig. 37) is more dorsal and narrower and the vinculum is shallower.

South Africa : Damaraland, Kuisip ; Transvaal. Southern Rhodesia : Mashonaland, Salisbury. Northern Rhodesia : Ft. Jameson.

Sesamia albivena Hampson.

Sesamia albivena Hampson 1902, Ann. S. Afr. Mus., **2**, p. 297.

Sesamia albavena (sic) Hampson, Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 330.

♂. Palpus white, infuscate. Antenna slightly serrate, cilia short, fasciculate. Head white, suffused with pink and infuscate above proboscis. Thorax white with flesh-pink suffusion, much paler posteriorly, tips of hairs on tegulae somewhat darkened. Legs white with pale pink or ochraceous-pink suffusion, fore tibia infuscate. Forewing flesh-pink, varying to white with pale pink suffusion, darkened to almost rufous at termen ; veins streaked with white, sometimes only slightly so ; some fuscous to fuscous-black markings variable in extent and intensity ; a sub-basal fuscous-black spot ; a diffuse longitudinal fuscous fascia from base along lower margin of cell, partly within it and partly without, extending almost to termen ; a fuscous-black spot at lower angle of cell, followed by a smaller one about the middle of the discocellulars ; a weak, curved postmedial fascia of small fuscous spots between the veins ; a narrow fuscous terminal line ; fringe white at base, moderately infuscate at tips. Hindwing white. Underside of forewing suffused pinkish-buff or buff along costa and termen with some fuscous irroration and a diffuse fuscous patch at apex of cell and a narrow fuscous terminal line ; fringe white, infuscate at tips. Underside of hindwing white with very pale buff suffusion along costa.

Expanse, 24–30 mm.

Male genitalia : tegumen with prominent peniculus. Valve (fig. 38) with sacculus and cucullus fused ; costal margin broadly sclerotised, costal spine large with lateral "wings" at apex ; sacculus very broad with a distinct "shoulder" ; cucullus small, narrow. Aedoeagus short, stout. Juxta with very large medial projection (fig. 39). Vinculum narrow, more or less triangular.

Female similar to male, forewing sometimes more purplish-pink ; expanse, 33 mm. Genitalia with anteostial pad large and heavily sclerotised, with a shallow indentation on posterior margin ; anterior lip of ostium heavily sclerotised.

South Africa : Transvaal ; White River, Kranspitz, Gemsbokfontein ; Natal, Estcourt. Southern Rhodesia : Mashonaland ; Salisbury, Umtali. Kenya : South Kavirondo. Uganda : Ruwenzori.

Sesamia albivena sudanensis, subsp. n.

♂. Palpus white with pale buff suffusion, and fairly heavily infuscate. Antenna simple, cilia short, fasciculate. Head light buff, sometimes infuscate. Thorax light buff, sometimes considerably infuscate anteriorly and with purplish-pink suffusion on humeri, faint pink suffusion on disc, and on propleuron. Pectus white, infuscate at base. Legs light buff, femora lightly, fore tibia heavily infuscate. Forewing light cartridge-buff to white with light buff suffusion, with a faint pink suffusion at base and narrowly along costa, termen with fuscous-buff suffusion : some fuscous markings variable in extent and intensity ; a sub-basal patch ; a fuscous-black spot at lower angle of cell with another smaller spot just distal to it ; a curved postmedial fascia of fuscous-black spots between the veins, the last spot most prominent ; a prominent black terminal line ; fringe white at base contrasting with the black terminal line, otherwise fringe infuscate. Hindwing white with pale pink suffusion along costa and termen and with a fuscous-black terminal line ; fringe white suffused with pink along costa, lightly infuscate at apex. Underside of forewing white suffused with pinkish-buff along costa, more fuscous towards termen ; a fuscous patch at apex of cell and a fuscous-black terminal line. Underside of hindwing white, apical half of costa suffused with pale buff and irrorate with fuscous ; a fuscous spot at the middle of the discocellulars, and a fuscous-black terminal line.

Expanse, 31 mm.

The male genitalia differ from those of *a. albivena* in that the costal spine of the valve (fig. 40) has less prominent apical ridges, terminating in a small hook, the cucullus lying at a flatter angle on the sacculus and the vinculum rounder, more like that of *S. cretica*. The juxta (fig. 41) has a large medial projection.

Female similar to male, but head and thorax sometimes white, with light buff suffusion and the thorax with less pink suffusion ; expanse, 33–34 mm. The genitalia differ from those of *a. albivena* in the much deeper excavation of the posterior lip of the anteostial pad.

Type ♂ : SUDAN : Temboura. 22.i.1919.

Allotype ♀ : SUDAN : Temboura. 7.xi.1918.

Paratypes : ♂, UGANDA : Amungo, Lango, 27.vii. 1935, at light (*H. B. Johnston*). CAMEROONS : Upper Uelle District, Dungu, —.vii.1939. NIGERIA : British Cameroons ; Kumba to Fumbo, 4,000 feet ; —.ix.1922.

Sesamia albivena mocoënsis, subsp. n.

♂. Palpus white with pale buff suffusion and light to moderate infuscation. Antenna serrate, cilia short, fasciculate. Head white sometimes suffused with pale buff and lightly streaked with fuscous. Thorax white, anteriorly with light ochraceous-buff or golden-buff suffusion. Pectus infuscate. Legs white with light buff to golden-buff suffusion, particularly the femora, the fore tibia moderately infuscate. Forewing white suffused with buff along costa and dorsum but more fuscous-buff towards the termen ; with some fuscous to fuscous-black markings variable in extent and intensity ; a sub-basal fuscous-black patch ; a small fuscous patch at the lower angle of the cell ; a curved postmedial fascia of small fuscous spots between the veins ; a narrow fuscous terminal line ; costal edge black ; fringe narrowly white at base, otherwise infuscate. Hindwing white, suffused with light fuscous along costa and apical half of termen, and with a narrow fuscous terminal line ; fringe white, infuscate at tips. Underside of forewing suffused with buff along costa, broadly suffused with light fuscous and irrorate fuscous towards termen, with a narrow fuscous-black terminal line ; fringe narrowly white at base, otherwise infuscate. Underside of hindwing white, costa and apex suffused with pale buff and irrorate with fuscous ; a narrow, light fuscous terminal line.

Expanse, 30–34 mm.

The valves (fig. 42) differ from those of *a. albivena* and *a. sudanensis* only in the less deeply excavated ridges of the costal spine. The juxta is shown in fig. 43.

Female unknown.

Type ♂ : PORTUGUESE EAST AFRICA : Luimbale, Mt. Moco, 1,800–1,900 m. 20.iii.1934 (*Dr. K. Jordan*).

Paratypes : 3 ♂♂, same locality and collector, 16–18.iii.1934.

S. taenioleuca and the three subspecies of *S. albivena* are considered together since they constitute a sharply defined natural group easily separable from *S. cretica* by the form of the juxta in the male and the anteostial pad in the female.

Although at first sight the completely pink *albivena albivena* and *taenioleuca* appear very distinct from *albivena sudanensis* and *albivena mocoënsis*, all four belong to one supraspecies * which has its northern limit more or less contiguous with the southern limit of *cretica* and extends almost as far south as the Cape. The subspecies with the most " typical " *Sesamia* facies is *albivena mocoënsis*, which is known at present from only one locality in Portuguese East Africa, and lacks all trace of pink suffusion. *S. a. sudanensis*, with some pink on thorax and wings, is the most northerly subspecies and is possibly contiguous with *cretica* at the southern limit of the latter ; in Uganda, it approaches *albivena albivena*, which spreads through East Africa south to Mashonaland and the Transvaal, where it overlaps *S. taenioleuca* which reaches Damaraland, the extreme south-western limit of the complex.

The biology of all these forms is unknown.

Sesamia rufescens Hampson.

Sesamia rufescens Hampson 1910, Cat. Lep. Phal. Brit. Mus., **9**, p. 329.

♂. Palpus white suffused with ochreous and considerably infuscate. Antenna serrate, cilia short, fasciculate. Head ochreous streaked with rufous. Thorax ochreous suffused with rufous. Pectus infuscate-ochreous. Legs ochreous suffused with rufous, the fore femora infuscate on the anterior surface. Abdomen ochreous suffused with rufous and infuscate on the posterior margins of each segment. Venter ochreous. Forewing ochreous, suffused with rufous, particularly below cell and along termen and inner margin ; a longitudinal fuscous fascia along lower margin of cell, partly within cell, partly without, extending to termen which is suffused with fuscous ; veins towards termen outlined with fuscous-black ; fringe fuscous-black. Hindwing white suffused with ochraceous at base and along costa, more fuscous towards termen ; fringe fuscous-black. Underside of hindwing white suffused with light ochraceous along costa, apex irrorate with fuscous ; fringe light fuscous.

Expanse, 28–30 mm.

Male genitalia of *cretica* type. Valve (fig. 44) with strong, hooked clasper (fig. 45) on inner surface ; costal spine flattened and expanded. Aedoeagus short and stout, manica with thickened serrate edges, and paired, ventral scobinate lobes. Juxta (fig. 46) with long blunt ventral projection.

Female similar to male, but less rufous, fringe more fuscous-brown ; expanse, 29–35 mm. Genitalia with bursa copulatrix more or less oval, and ductus bursae long, narrowly sclerotised at base ; anteostial pad very small ; ostium with anterior lip fairly heavily sclerotised ; ostial segment with sclerotised band behind ostium divided in medial line.

South Africa : Natal ; Durban, Mooi River, Stanger, Zululand. Northern Rhodesia : Gimson.

S. rufescens is easily separated from all other species in the genus by its bright rufous colour, the well developed clasper on the valve (a unique character in *Sesamia*) and the reduced anteostial pad in the female. It is reminiscent of *Busseola* in the very broad valve, with its clasper, and the strongly sclerotised anterior lip of the ostium.

Biology unknown.

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* It appears that *S. taenioleuca* and the subspecies of *S. albivena* constitute a group analagous to the *Diatraea rosa*—*Diatraea busckella* complex discussed by Box (1951).

OTHER SPECIES OF SESAMIA RECORDED FROM AFRICA.

(1) **Sesamia tosta** Snellen 1872 (Tijdschr. Ent., **15,** p. 50, pl. IV, fig. 8) described from the Congo, is unidentifiable from its description or figure. No specimens of this species have been seen, but if it is a *Sesamia* it is most probably *S. calamistis*. If this should be correct, the name *tosta* would normally take priority. There would, however, be a strong case for the suppression of *tosta* in favour of *calamistis*.

(2) **Sesamia sabulosa** Hampson 1910 (Cat. Lep. Phal., **9,** p. 328). This species is not a *Sesamia*, but belongs to an apparently undescribed genus, near *Sesamia* but differing in venation and the structure of the genitalia.

(3) **Sesamia atlantica** Boursin 1944 (Rev. franç. Ent., **10,** p. 167, pl. V, figs. 13, 16). No specimens have been seen, but the locality (Morocco) and Boursin's figure suggest that this is a subspecies of *Sesamia jansei*.

(4) **Sesamia albicolor** Janse 1939. Moths S. Afr., **3,** p. 376.

(5) **Sesamia sylvata** Janse 1939. Moths S. Afr., **3,** p. 377.

No specimens of these two species have been seen.

FURTHER CLARIFICATION OF PAST CONFUSION.

As far as possible, the tangles in the applications of the older names of these moths, whose larvae bore in graminaceous plants, have been unravelled, but it may be well to add a special illustrated note to ensure that the facts are viewed in the proper perspective.

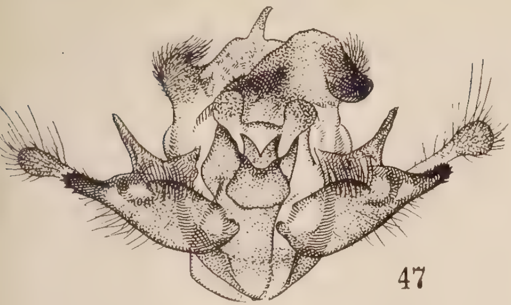
A species over which there has been much confusion is the one which seems to have come to rival *Busseola fusca* (Fuller) in economic importance, *viz.*, *Sesamia calamistis* Hampson, which is illustrated in figs. 47, 48, 70, 71 and 72 ; figs. 70 and 72 are photographs of Hampson's and Janse's figures, respectively, which were erroneously stated by these authors to represent *vuteria*. Janse also used the name *vuteria* erroneously for the insect whose male genitalia are shown in fig. 73 (Janse's figure), and now named *Sesamia jansei* Tams & Bowden. The differences between *S. calamistis* Hampson (figs. 47 and 48) and *S. jansei* Tams & Bowden (figs. 49 and 50) are easily recognisable from genitalia preparations, and the males are readily distinguishable by the antennae (figs. 51 and 52).

Figs. 60, 61 and 62 should serve to eradicate from the true *Sesamia* spp. the misnomer "*vuteria*" auctorum, and establish *vuteria* firmly in the new genus *Speia* Tams & Bowden in its proper application as *Speia vuteria* (Stoll), of which the genitalia of both sexes are shown in figs. 53 and 54.

With regard to *Conicofrontia* Hampson, the original description of this genus was based on *C. sesamoides* Hampson 1902 (Ann. S. Afr. Mus., **2,** p. 296). (The redescription of the genus in Cat. Lep. Phal., **9,** p. 338, 1910, resulted from the erroneous attribution to this species by Hampson of the male *Speia vuteria* (Stoll) figured by him under the name "*Conicofrontia sesamiodes* [*sic*]," ♂, and should be disregarded.) Unfortunately, Hampson (Cat. Lep. Phal., **9,** p. 272, 1910) also described *C. sesamoides* under the name *Phragmatiphila bipartita*. It is not a *Phragmatiphila*. We now know that *P. bipartita* is the male of *C. sesamoides* (see figs. 66 and 67) ; the structure of the genitalia is shown in figs. 55 and 56.

Leucania incerta Walker 1856 (List Lep. Ins. Brit. Mus., **9,** p. 103) is obviously a *Sesamia* (see figs. 63 and 74) ; Walker gives South Africa as its place of origin, but we have so far failed to find a match for it. *Nonagria sacchari* Wollaston is evidently *S. nonagrioides* (Lefebvre) (fig. 64), and *Sesamia mediastriga* Bethune-Baker from Angola is *S. calamistis* Hampson (fig. 65).

Sesamia botanephaga Tams & Bowden, the large West African species, is represented in figs. 57 and 58.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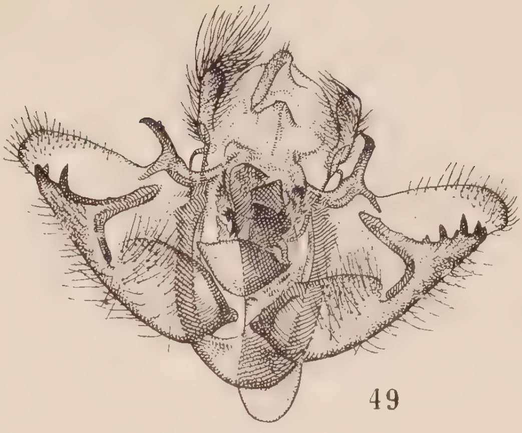
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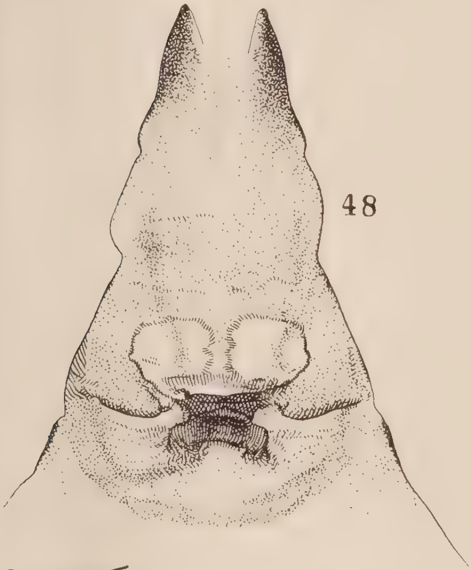
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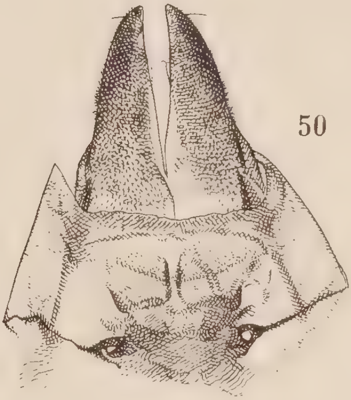
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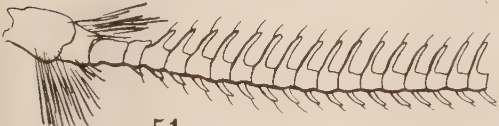
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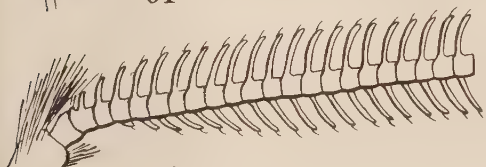
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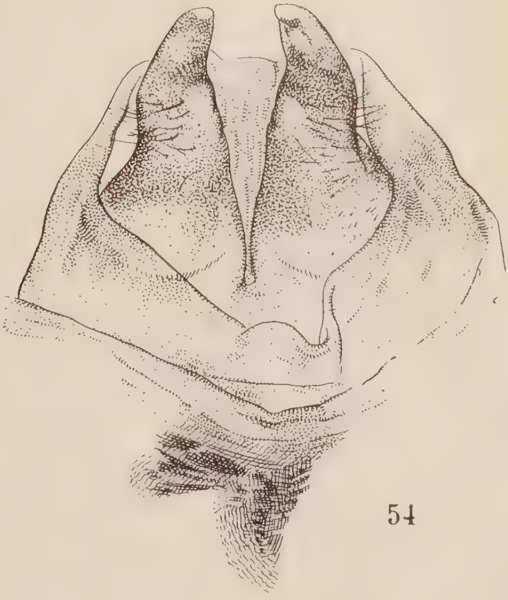
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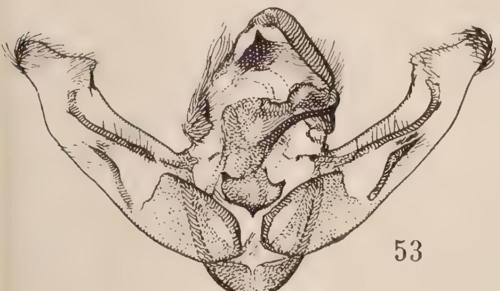
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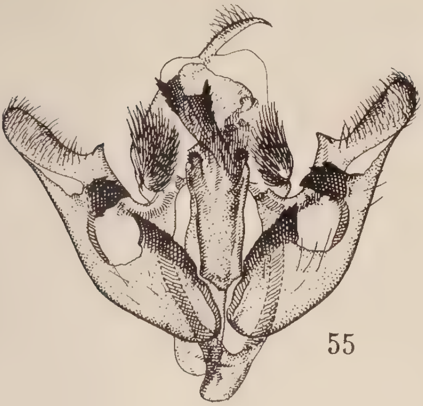
Sesamia calamistis Hampson. Fig. 47, male genitalia; Fig. 48, female genitalia.
Sesamia jansei, sp.n. Fig. 49, male genitalia; Fig. 50, female genitalia.
Sesamia calamistis Hampson. Fig. 51, antenna of male.
Sesamia jansei, sp.n. Fig. 52, antenna of male.
Speia vuteria (Stoll). Fig. 53, male genitalia; Fig. 54, female genitalia.



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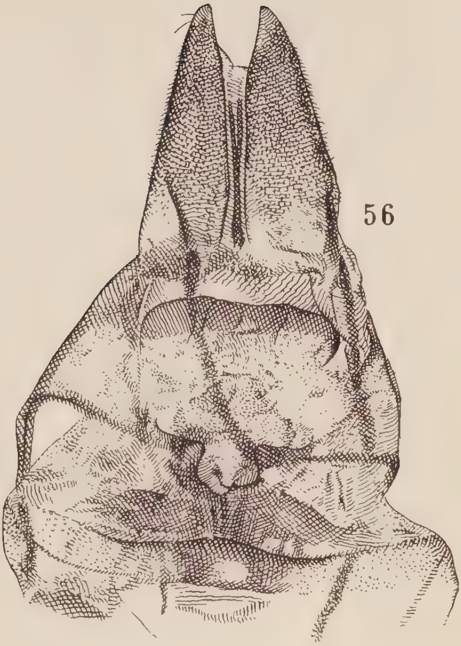

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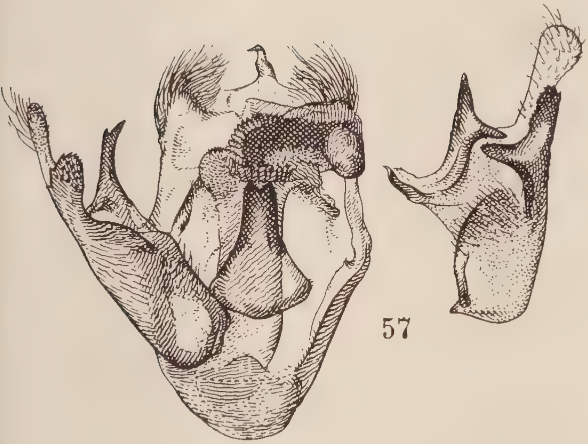

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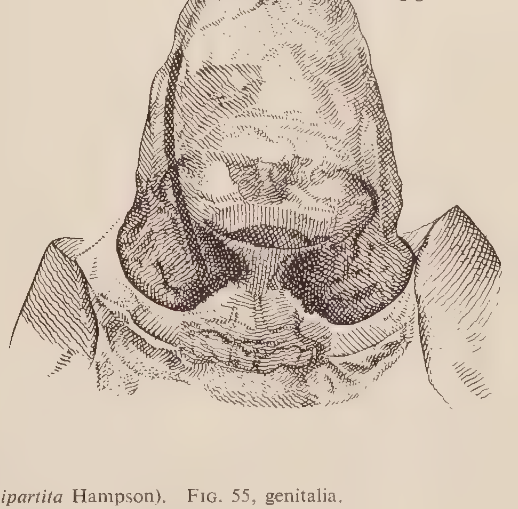

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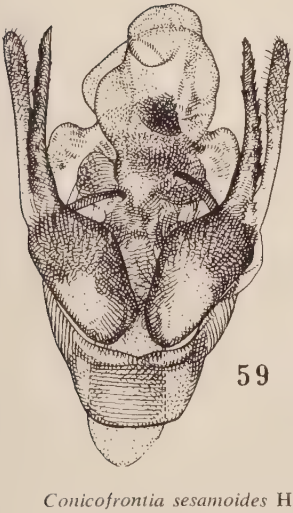

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Conicofrontia sesamoides Hampson (male *bipartita* Hampson). FIG. 55, genitalia.
Conicofrontia sesamoides Hampson. FIG. 56, female genitalia.
Sesamia botanephaga, sp.n. FIG. 57, male genitalia; FIG. 58, female genitalia.
Sesamia oriaula, sp.n. FIG. 59, male genitalia.

We have included photographs of the wings of *Poeonoma similis* Tams & Bowden (fig. 68) and *Busseola fusca* (Fuller) (fig. 69), for it would be quite easy for even an experienced lepidopterist to confuse these if he were not in a position to put them side by side for comparison.

After this paper had been prepared a single male example of another species was found among unworked material in the British Museum ; this resembled so closely the *calamistis–jansei* group, and could so easily be determined as one of these on a casual examination, that it was decided to include it in this paper with a figure of the male genitalia. This species, which is described below, could be detected immediately without making a special preparation, as the sacculus can be exposed to view by brushing back the terminal scales of the abdomen.

Sesamia oriaula, sp. n.

♂. A species resembling *S. calamistis* and *S. jansei*, but more richly coloured, slightly larger than *S. calamistis*, readily distinguished by the male genitalia, in which the cucullus and sacculus are about equal in length, the latter narrow, outwardly serrate, and pointed (fig. 59). Holotype ♂.—UGANDA : Ruwenzori Range, Bwamba Pass, west side, 5,500– 7,500 feet, xii.1934–i.1935 (*F. W. Edwards*).

Acknowledgements.

One of us (J. B.) is indebted to the Director of Agriculture, Gold Coast, and the Gold Coast Government for an extension of leave which made this work possible ; also to Professor J. E. Harris, Department of Zoology, University of Bristol, for permission to work in his Department. To Dr. W. J. Hall, C.M.G., M.C., and Dr. T. H. C. Taylor of the Commonwealth Institute of Entomology thanks are due for their interest and help during the course of this investigation. We are both greatly indebted to Professor A. J. T. Janse of Pretoria for the loan of his specimens and slides, and to Mr. Arthur Smith for figs. 47–50 and 53–59.

Summary.

The primary object of the work which is the subject of this paper was to clarify the confusion that has existed for many years in the nomenclature and taxonomy of certain important Agrotid borers of graminaceous crops in Africa.

The genera involved are *Speia*, *Sciomesa*, *Poeonoma*, *Conicofrontia*, *Busseola* and *Sesamia*, and of these the first three are new and are described and the others are redescribed. A key to the genera and keys to the species of *Sciomesa*, *Poeonoma* and *Sesamia* are given. The genus *Speia* is erected for *Phalaena vuteria* Stoll ; the name *vuteria* Stoll has been wrongly applied to the important pest of sugar-cane in Mauritius, which is, in fact, the well known *Sesamia calamistis* Hampson. *Sciomesa* is erected to contain three species previously included in *Conicofrontia*. *Poeonoma* also contains three species, of which one is *Phragmatiphila serrata* Hampson and the other two are new. Hampson's species *Conicofrontia sesamoides* is redescribed in *Conicofrontia* and is the only species of that genus dealt with in detail ; *Phragmatiphila bipartita* Hampson is synonymised with it. In the genus *Busseola*, only the well known pest, *B. fusca* (Fuller) is described.

In *Sesamia*, 15 species and two subspecies are described ; six of the species and both of the subspecies are new. (One of the new species is described separately at the end of the paper and is not included in the key.) The new species include *botanephaga*, a serious pest of maize in W. Africa ; this has hitherto been erroneously treated as *Sesamia calamistis* Hampson, which is one of the species redescribed. *S. cretica* Lederer, another species dealt with at length, is a pest of maize and sorghum in the Mediterranean area.

The synonymy and distribution of each species are given and its food-plants recorded if known. Figures of important diagnostic features, especially genitalia, are included.

A separate section provides supplementary notes and illustrations to clarify further the most complicated of the problems that have arisen through past errors of identification and nomenclature.

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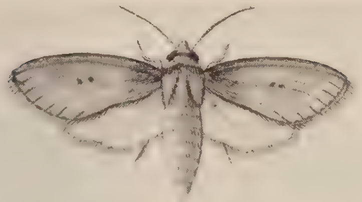
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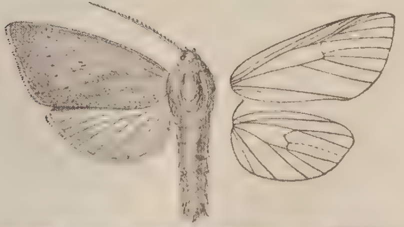
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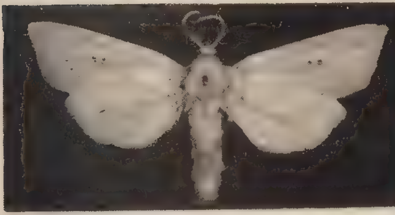
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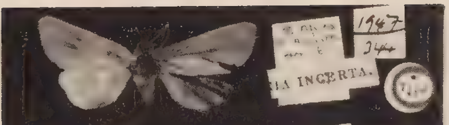
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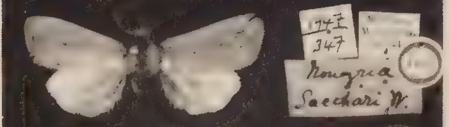
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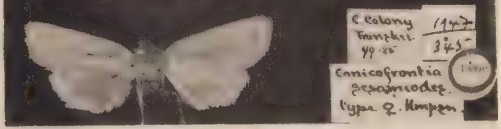
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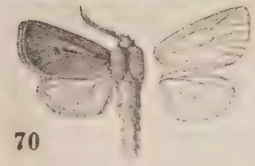
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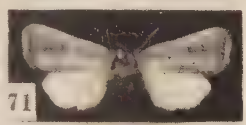
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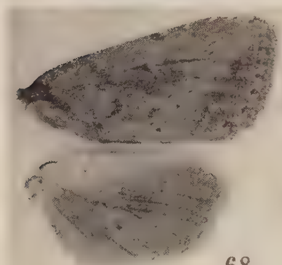
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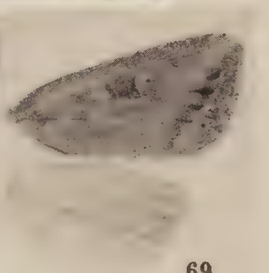
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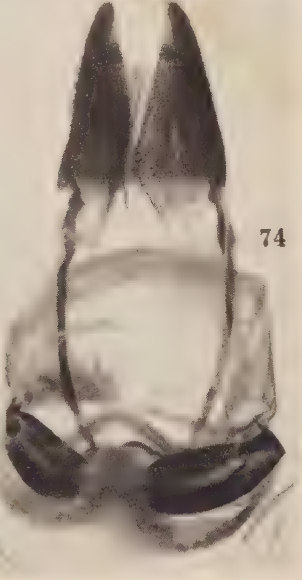
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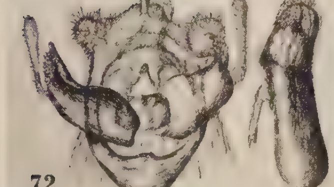
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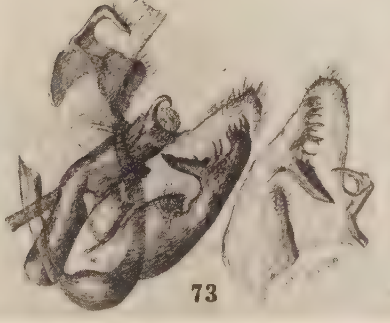
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FIG. 60. *Speia vuteria;* Stoll's original figure. FIG. 61. *Speia vuteria* (Stoll); Hampson's figure of the male which he called in error "*Conicofrontia sesamiodes*" [sic]. FIG. 62. *Speia vuteria* (Stoll); a photograph of a specimen of the true *vuteria* Stoll for comparison with drawings shown in FIGS. 60 and 61. FIG. 63. The type of *Leucania incerta* Walker, which is a *Sesamia*. FIG. 64. The type of *Nonagria sacchari* Wollaston, which is *Sesamia nonagrioides* (Lefebvre). FIG. 65. The type of *Sesamia mediastriga* Bethune-Baker, which is *Sesamia calamistis* Hampson. FIG. 66. *Conicofrontia sesamoides* Hampson, ♂ ; described by Hampson as *Phragmatiphila bipartita*. FIG. 67. *Conicofrontia sesamoides* Hampson, type ♀ ; the female described by Hampson as *C. sesamoides* (not as he labelled it, "*sesamiodes*"). FIG. 68. Wings of *Poeonoma similis* Tams & Bowden, sp.n. FIG. 69. Wings of *Busseola fusca* (Fuller). FIG. 70. *Sesamia calamistis* Hampson; Hampson's figure which he called "*vuteria*" in error. FIG. 71. *Sesamia calamistis* Hampson; the type male. FIG. 72. *Sesamia calamistis* Hampson; Janse's figure of the male genitalia, called "*vuteria*" in error. FIG. 73. *Sesamia jansei* Tams & Bowden, sp.n.; Janse's figure of the male genitalia, called "*calamistis*" in error. FIG. 74. Genitalia of the type female of *Leucania incerta* Walker (see FIG. 63), which is a *Sesamia*.

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SOME IMPORTANT SPECIES OF THE GENUS *CRYPTOPHLEBIA* WALSINGHAM, 1899, WITH DESCRIPTIONS OF THREE NEW SPECIES (LEPIDOPTERA : OLETHREUTIDAE).

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(Plates XXIV & XXV.)

A great deal of confusion has arisen in the past over the identities of the adults of certain species of the genus *Cryptophlebia* which, because of the damage they cause as larvae, are economically important. The original descriptions of them are widely scattered in the literature and are often in journals that are not readily available. In the present paper, these species are brought together to facilitate comparison. At the same time, all the other known species congeneric with them are assembled, many being new assignments to the genus, and some of the salient specific characters for each are given. The identifications of the species mentioned are based on type and other material in the British Museum.

The species over which confusion has arisen are *ombrodelta* Lower, which name replaces the familiar *carpophaga* Wals. because it is earlier, *illepida* Butler, *peltastica* Meyrick, *praesiliens* Meyrick, *rhynchias* Meyrick, *vitiensis*, sp. n., *williamsi*, sp. n. and *pallifimbriana*, sp. n. Two of them, *ombrodelta* and *illepida*, were considered by many authors to be synonymous until they were finally separated by Swezey & Zimmerman (1946, Proc. Hawaii. ent. Soc., **12,** p. 629). Unfortunately, the confusion goes much deeper than this. The series labelled *ombrodelta* in the British Museum was found to contain examples of four of the other species mentioned above, many bearing Meyrick's determination label, while examples of *ombrodelta* were in the series labelled *peltastica* and that labelled *illepida*. It is certain that some of the identifications made from this material in the past are erroneous, and it would be advisable to verify the identity of specimens that have been determined as any of them.

Our knowledge of the genus *Cryptophlebia* is still very incomplete, and it is thought inadvisable at this stage to construct a key for the separation of the 18 species known. Some of them are represented by the type only or by examples of one sex only. Furthermore, when the species in *Argyroploce* Hübner are adequately investigated, more will probably be found to belong to *Cryptophlebia.*

As far as is known, the eight species mentioned above are the most important economically and are the ones most often encountered where they occur. On the basis of superficial characters, they fall into two groups, and the species in each group can be separated from each other according to geographical distribution. One group comprises *ombrodelta, illepida, peltastica* and *vitiensis,* and although these are very much alike superficially (Pl. XXIV), each occurs in a different region, *ombrodelta* being Australasian, *illepida* Hawaiian and *vitiensis* Fijian, while *peltastica* is found in South Africa, Madagascar and the Seychelles. The other group contains *rhynchias, praesiliens, williamsi* and *pallifimbriana,* and these can likewise be separated by their geographical distribution, except for an overlapping of *rhynchias* and *pallifimbriana* in the New Hebrides. A chart to show the known distribution of all the species assigned herein to the genus *Cryptophlebia* is given.

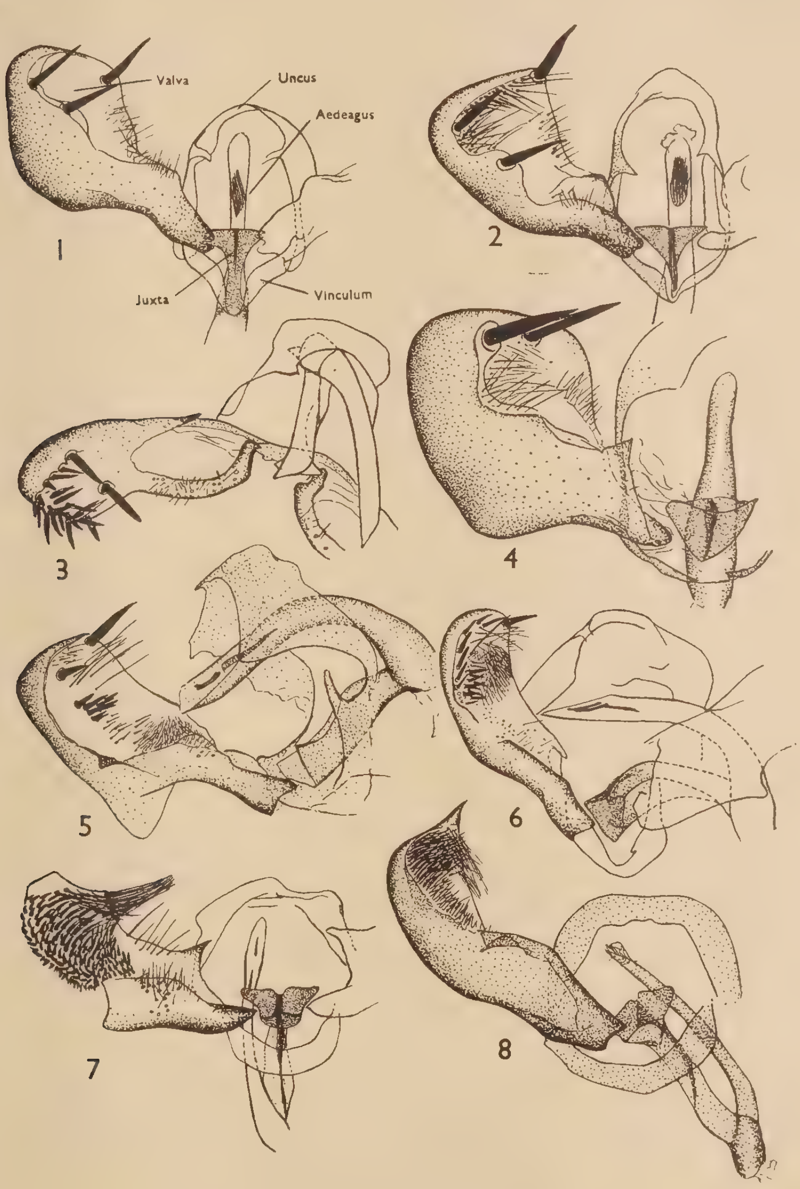
In the species examined, the female is on the whole larger and has better defined markings than the male. A female of each species has therefore been used for the illustrations on Plate XXIV. The markings on the forewing of the male were found

Distribution of species of *Cryptophlebia*.

	ombrodelta (*carpophaga*)	*peltastica*	*socotrensis*	*vitiensis*	*iilepida*	*iridosoma*	*distorta*	*lasiandra*	*repletana*	*strepsibathra*	*phaeacma*	*toxogramma*	*encarpa*	*praesiliens*	*williamsi*	*rhynchias*	*pallifimbriana*	undescr. sp. see *lasiandra*	*carpophagoides*
Africa		×												×					
Madagascar ...		×													×				
Mauritius ...		×													×				
Seychelles ...		×																	
Sokotra			×																
India	×								×				×			×			
Ceylon	×							×					×			×			
China							×												
Formosa ...	×								×										
Siam ...	×																		
Philippines ...	×								×										
Guam	×	×																	
Sarawak... ...									×										
W. Celebes ...									×										
Sumatra ...									×										
Indonesia ...	×																		
New Guinea ...									×			×					×		
Vulcan I. ...																	×		
Dampier I. ...	×																		
Rook I. ...												×							
New Hanover ...													×						
New Ireland ...									×										
New Britain ...										×	×								
St. Aignan ...													×						
Rossel I. ...						×						×							
Sudest I. ...												×	×			×			
Marquesas ...																	×		
Austral Is. ...																	×		
Society Is. ...																	×		
New Hebrides ...																×	×		
Fiji				×					×								×	×	
Tahiti																	×		
Hawaii					×														
Australia ...	×					×										×			
S. Am.(Argentina)																			×

to be usually less distinct, and in some examples the characteristic pretornal marking on the dorsum is absent or, as is more often the case, poorly defined. The male of some species is adorned with special secondary sexual characters, such as a tuft of hair on the hind tibia, or a specialised pocket or brush of scales at the inner angle of the hindwing.

The genitalia of both sexes show excellent specific characters. The male genitalia (figs. 1–8) are fairly large and, if the covering scales are removed with a moistened camel-hair brush, can be examined with a strong (×20) hand-lens. The number and disposition of the spine-like setae on the valva is a fairly stable character and enables



Male genitalia of *Cryptophlebia* spp., ventral view.

Fig. 1.—*ombrodelta* (Lower) ; 2—*peltastica* (Meyr.) ; 3—*illepida* (Butler) ; 4—*vitiensis*, sp. n. ; 5—*pallifimbriana*, sp. n. ; 6—*rhynchias* (Meyr.) ; 7—*praesiliens* (Meyr.) ; 8—*williamsi*, sp. n.

most of the species to be readily distinguished. The female genitalia (Pl. XXV, figs. 1–8) are best examined after immersion in 10 per cent. caustic potash. The structure of the genital plate and the size, shape and position in the bursa copulatrix of the signa are important diagnostic characters for each species.

The food-plants are given where known, but our knowledge of them is very incomplete. The larvae are mostly borers, in pods, fruits, seeds or stems. The immature stages of species that occur in Mauritius are described in a paper by Mr. J. R. Williams (see the following paper in this *Bulletin*, p. 691) who has kindly presented series of reared specimens in fine condition to the British Museum.

The types and paratypes of the new species described below are in the British Museum.

Genus **Cryptophlebia** Walsingham, 1899.

Cryptophlebia Walsingham, 1899, Indian Museum Notes, **4,** p. 105.

Type species : *Cryptophlebia carpophaga* Walsingham.

Pogonozada Hampson, 1905, Ann. Mag. nat. Hist., (7) **16,** p. 586.

Type species : *Pogonozada distorta* Hampson.

Cryptophlebia ombrodelta (Lower), new combination.

Arotrophora (?) *ombrodelta* Lower 1898, Proc. Linn. Soc. N.S.W., **23,** p. 48.

Cryptophlebia carpophaga Walsingham, 1899, Indian Museum Notes, **4,** p. 106.

Adult ♀ illustrated on Pl. XXIV, fig. 1.

The forewing in the female is reddish-tawny, and has a conspicuous, dark reddish-tawny marking, which in some examples is crossed by a fuscous dash, near the tornus on the dorsum. In the male, the forewing is tawny, a blackish suffusion extends along the dorsum, the tornal area is lightened by an admixture of bone-grey scales, and the pretornal spot on the dorsum is often indistinct. The hindwing in the male has a dense subdorsal brush of hairs on the upper surface, and the hind tibia has a dense blackish fuscous tuft on the inner surface.

Wing expanse, 15–22 mm.

Male genitalia, fig. 1.

Female genitalia, Pl. XXV, figs. 1 & 1a.

Distribution : South India, Ceylon, Formosa, Indonesia (Java), Siam, Philippine Is., Guam, Dampier I., Australia (Queensland, N.S. Wales, and N. Territory).

Food-plants : *Parkinsonia aculeata* (leaves and pods), *Cassia fistula* and *C. occidentalis* (pods), litchi (fruits and seeds), various species of *Acacia* (pods and seeds), *Aegle marmelos* (fallen fruits), *Sesbania aculeata* (pods), *S. grandiflora* (seeds), tamarind (fruits), *Feronia* (fruits), *Bauhinia purpurea* (pods), orange (fruits), *Adenanthera pavonia* and *Pithecolobium dulce.*

Cryptophlebia peltastica (Meyrick), new combination.

Argyroploce peltastica Meyrick, 1921, Ann. Transvaal Mus., **8,** p. 57.

This identification is based on the female paratype in Meyrick's collection in the British Museum, the type being in the Transvaal Museum and not available.

The series of specimens labelled *peltastica* in Meyrick's collection and in the British Museum were found, when examined, to include specimens of *praesiliens* Meyrick, while specimens of *peltastica* bearing Meyrick's determination label had been misidentified by him as *ombrodelta* or its synonym *carpophaga*. It therefore seems evident that all specimens identified as any of these species, even when determined by Meyrick himself, need to be re-examined and to have their identity verified.

Adult ♀ illustrated on Pl. XXIV, fig. 2.

Forewing light brownish clay, in the female irregularly suffused with greyish-fuscous which darkens the wing of some examples considerably and gives it a rather leaden and variegated appearance ; pretornal spot on dorsum vinaceous, present in both sexes but usually better defined and more richly coloured in the female, crossed by two light brown lines and surrounded on its inner side by a thin whitish line. The male has only a small brush of hair on the surface of the hindwing, but the inner margin is fringed with long hairs and scales. The tuft on the hind tibia is considerably larger and denser than that in *ombrodelta* and *carpophagoides*.

Wing expanse, 16–26 mm.

Male genitalia, fig. 2. Distinguishable from those of *ombrodelta* by the small setae between the two large, strong setae in the distal margin of the valva. The dense cluster of cornuti in the aedeagus is deciduous.

Female genitalia, Pl. XXV, figs. 2 & 2a (paratype genitalia, B.M. slide 1923). Anterior edge of eighth tergite incurved.

Type in the Transvaal Museum.

Distribution : Africa (Eritrea, Nyasaland, Pondoland, Durban), Seychelles, Madagascar, Mauritius; also recorded from Guam.

Food-plants : Litchi (fruits), carob (*Ceratonia siliqua*) (pods) Flamboyant tree (*Poinciana regia*) (stems), *Tamarindus indica, Bauhinia* sp. (pods) ; also from *Canavalia ensiformis* (according to Meyrick, 1930, Trans. ent. Soc. Lond., **78** p. 311).

Cryptophlebia socotrensis Walsingham.

Cryptophlebia socotrensis Walsingham, 1900, Bull. Liverpool Mus., **3**, p. 6.

Described from a female specimen taken on the Island of Sokotra. This specimen was the unique type and presumably came to the British Museum with the Walsingham collection, but it cannot now be traced; it was listed by J. H. Durrant, but not by H. Stringer.

Cryptophlebia vitiensis, sp. n.

Adult ♀ illustrated on Pl. XXIV, fig. 4 (allotype).

Head, labial palpus, antenna, thorax and forewing a warm reddish brown, preapical and tornal area of forewing lightly suffused with bone white, a small bone-white spot in the middle of forewing, pretornal mark on dorsum dark reddish-brown with inner edges whitish. Hindwing greyish brown. In the forewing of the male, the pretornal spot is almost obsolete ; the hindwing has a special brush of scales similar to that in *ombrodelta*, and the hind tibia has a brush of dense, fuscous scales, a little larger than that in *ombrodelta*, ochreous outwardly and blackish fuscous inwardly.

Wing expanse, 18–24 mm.

Male genitalia, fig. 4 (holotype genitalia, B.M. slide 1933).

Female genitalia, Pl XXV, figs. 4 & 4a (allotype genitalia, B.M. slide 1935).

Holotype ♂ : " Fiji, Vunidawa, 23.12.1932, *H. Phillips* ".

Allotype ♀ : " Fiji, Vunidawa, 30.1.1933, *H. Phillips* ".

Paratypes : 2♂, 2♀ ; all " Fiji ", two " Vunidawa " dated " 9.12.32 " and " 4.1.32," respectively, and collected by " *H. Phillips* ", one " 1933, *H. Phillips* " and one " Suva, 22.3.23, at light, *H. W. Simmonds* ".

Distribution : Fiji.

Food-plants : not known.

Cryptophlebia illepida (Butler).

Teras illepida Butler, 1882, Trans. ent. Soc. Lond., **1882** p. 42.

Cryptophlebia fulva Walsingham, 1907, Fauna Hawaiiensis, **1** p. 681.

Cryptophlebia suffusa Walsingham, 1907, Fauna Hawaiiensis, **1** p. 682.

Cryptophlebia tetrao Walsingham, 1907, Fauna Hawaiiensis, **1** p. 683.

Cryptophlebia vulpes Walsingham, 1907, Fauna Hawaiiensis, **1** p. 683.

Adult ♀ illustrated on Pl. XXIV, fig. 3.

Forewing a tawny brown, pretornal spot dull reddish-brown, a little smaller than in *ombrodelta* and not so conspicuous. This species is variable and has a number of widely different colour forms. In the male, the pretornal spot is sometimes absent, but often there is a slight infuscation in its place. The hindwing of the male has the special brush of sexual scales at the inner angle as in *ombrodelta ;* the hind tibia has a tuft of dense scales similar to that in *ombrodelta* and *vitiensis* except that in them it is fuscous-black inwardly, while in *illepida* it is ochreous with only a slight admixtúre of fuscous.

Wing expanse, 14–21 mm.

Male genitalia, fig. 3.

Female genitalia, Pl. XXV, figs. 3 & 3a.

Distribution : Hawaiian Is.

Food-plants : *Acacia koa* (pods), and probably several other leguminous trees and plants. (Biology and early stages described by Swezey, 1908, Proc. Hawaii. ent. Soc., **2** p. 14.)

Cryptophlebia iridosoma (Meyrick), new combination.

Argyroploce iridosoma Meyrick, 1911, Proc. Linn. Soc. N.S.W., **36** p. 264.

A smaller species than *ombrodelta* and with very different male genitalia. The valva is elongate and has a solitary large spine-like seta surrounded by long slender setae at the edge of the margin distally, but, because of the shape of the valva, these setae appear at first sight to be situated near the middle and not at the margin of the valva; along the ventral margin is a patch of minute tooth-like setae and basad to these, a little above the sacculus, is a fairly stout seta.

Wing expanse, 14–16 mm.

Distribution: Australia (lectotype " Brisbane, Queensland, K.S.T. .12.05 ". Genitalia B.M. slide 2453); Rossel I.

Food-plants: not known.

Cryptophlebia distorta (Hampson), new combination.

Pogonozada distorta Hampson, 1905, Ann. Mag. nat. Hist., (7) **16,** p. 586.

Known only from the unique type, a male. Previously synonymised under *ombrodelta* to which it is superficially similar in some respects.

The male genitalia are distinctive. The valva has seven or eight long slender setae unevenly distributed in the distal margin, and a compact row of nine or ten very small spine-like setae ventrally; it lacks the three large setae found in *ombrodelta* and *lasiandra*. (Genitalia, B.M. slide 1905.)

Wing expanse, 17 mm.

Distribution : China (Type ♂ " Ichang, *Mrs. Pratt*, Aug. 1888 ").

Food-plants : not known.

Cryptophlebia lasiandra (Meyrick), new combination.

Argyroploce lasiandra Meyrick, 1909, J. Bombay nat. Hist. Soc., **19,** p. 592.

Described by Meyrick from a male specimen taken in November at Trincomali, Ceylon. The genitalia are very similar to those of *ombrodelta* but are distinguishable by two small spine-like setae, not present in *ombrodelta*, between the two furthermost large stout setae and a little nearer to the one situated dorsad.

This species was also recorded by Meyrick (1925, Exot. Microlep., **3** p. 143) from Fiji, on the basis of a specimen bred from the hypercotyl of seedlings of *Bruguiera Rheedi* (a mangrove), but the genitalia of this specimen differ from those of the type of *lasiandra*. The Fijian specimen almost certainly represents a new species, but it seems best not to describe it until adequate material is available.

Distribution : Ceylon.

Food-plants : not known.

Cryptophlebia repletana (Walker), new combination.

Carpocapsa repletana Walker, 1863, List Lep. Ins. B.M., **28** p. 412 .

Argyroploce trichosema Meyrick, 1914, Suppl. Ent., **3** p. 48 (**syn. nov.**).

Argyroploce tetraploca Meyrick, 1928, Exot. Microlep., **3** p. 446 (**syn. nov.**).

This species is widely distributed in S.E. Asia and the Pacific Islands. Its similarity to the next species, *strepsibathra*, which occurs in New Britain, and the difficulty of separating them without critical examination, rather suggests that more than one species or subspecies might be involved.

The type of *repletana* is from Sarawak, that of *tetraploca* is from the Philippines, and *trichosema* is from Formosa.

This species does not appear to vary very much superficially, and there is no marked contrast between the sexes. The examples examined conform to the descriptions by Walker and Meyrick (*l.c.*).

Wing expanse, 18–24 mm.

Distribution : S. India, Formosa, Philippines, W. Celebes, Sarawak, New Guinea (Papua), Sumatra, New Ireland, Fiji.

Food-plants : not known.

Cryptophlebia strepsibathra (Meyrick), new combination.

Argyroploce strepsibathra Meyrick, 1928, Exot. Microlep., **3** p. 446.

Known only from the type, a male. Closely related and superficially very similar to *repletana*.

The valva of the male genitalia has a large solitary spine-like seta on the inner margin of the costa near the apex ; opposite this in the ventral margin is a short, very stout seta, and near this towards the base of the valva are two smaller setae set side by side, one much smaller than the other, the larger being nearer the base.

Wing expanse, 20 mm.

Distribution : New Britain. (The type bears the data " Talesea, A.F.E. .1.25.")

Food-plants : Soybean (stems).

Cryptophlebia phaeacma (Meyrick), new combination.

Argyroploce phaeacma Meyrick, 1931, Exot. Microlep., **4** p. 129.

Known only from the type, a male. Allied to *strepsibathra* but has not the peculiar secondary sexual characters of that species, and in the forewing the pretornal spot is almost obsolete.

The male genitalia have two large spine-like setae on the valva, one situated at the apex and the other distally, a small spine-like seta near the ventral margin and a number of long setae in the middle area of the valva.

Wing expanse, 23 mm.

Distribution : New Britain. (The type bears the data " Talesea, A.F.E. .2.25 ".)

Food-plants : not known.

Cryptophlebia encarpa (Meyrick), new combination.

Argyroploce encarpa Meyrick, 1920, Exot. Microlep., **2** p. 349.

Except for one male, believed to be conspecific, only female examples of this species are known. The structure of the genitalia of the male is very distinctive ; the valva is in the form of an elongate scoop and has a row of six evenly distributed medium-sized spine-like setae in the ventral margin, and numerous long, slender setae dorsad of these.

Wing expanse, 16–18 mm.

Distribution : S. India, New Hanover, Sudest I.

Food-plants : *Zizyphus jujuba* (fruits), the fruit and leaves being webbed ; Tangerine orange (fruit).

Cryptophlebia toxogramma (Meyrick), new combination.

Argyroploce toxogramma Meyrick, 1924, Exot. Microlep., **3** p. 143.

In general appearance somewhat suggestive of *repletana* but considerably larger, and with the coloration of the forewing tawny and not brown, and without the pretornal spot on the dorsum.

The genitalia of the male have the valva armed with one large spine-like seta situated dorsally before or at the apex, two about half the size distally, and one or two of the same size midway along the ventral margin.

Wing expanse, 28 mm.

Distribution : New Guinea, Rook I., Rossel I., Sudest I.

Food-plants : not known.

Cryptophlebia praesiliens (Meyrick), new combination.

Argyroploce praesiliens Meyrick, 1924, Exot. Microlep., **3** p. 68.

Argyroploce xylodelta Meyrick, 1928, Exot. Microlep., **3** p. 444 (**syn. nov.**).

Adult ♀ illustrated on Pl. XXIV, fig. 7.

Head, labial palpus and thorax ochreous brown. Forewing brown, weakly clouded with a dark grey suffusion, costa lightly strigulated, a black dash above dorsum before the tornus, a cloudy streak of ochreous-whitish suffusion along apical half of termen, backed inwardly by a dark brown somewhat triangular mark ; tornal area suffused ochreous-whitish ; cilia in apical half barred with brown. In the male, the forewing is lighter and without the greyish clouding ; the pretornal mark is reduced to a few fuscous scales or is sometimes completely absent.

Wing expanse, 17–26 mm.

Male genitalia, fig. 7.

Female genitalia, Pl. XXV, figs. 7 & 7a.

Distribution : Africa (Uganda, Tanganyika Territory, Natal).

Food-plants : This species is commonly referred to as the " Raintree borer"; it lives in a species of *Sesbania*.

Cryptophlebia williamsi, sp. n.

Adult ♀ illustrated on Pl. XXIV, fig. 8 (allotype).

Head, labial palpus, thorax and forewing light brown, heavily suffused and overlaid with greyish fuscous giving the whole a faintly purplish bloom, tornal area of forewing suffused with ochreous irrorated with a few specks of fuscous, a minute but conspicuous white discal spot ; pretornal mark on dorsum fuscous obliquely broken or cut; a large elongate spot beneath apex at termen greyish ochreous suffused with pale olive green, except for inner margin, and broadly edged with fuscous inwardly. Cilia light brown, four distinct brown lines with a pinkish tint rising from terminal spot, several indistinct brownish lines at tornus. Hindwing brownish fuscous ; cilia dark brown at base and light brown at extremities, tinged with pink along termen.

In the male, the forewing has a faintly greenish-ochreous or sometimes brownish-ochreous coloration with a faint infuscation, and is altogether a much lighter colour than in the female, but is otherwise similar except that the dorsal spot is greatly reduced and in some examples is absent.

Wing expanse, 20–31 mm.

Male genitalia, fig. 8.

Female genitalia, Pl. XXV, figs. 8 & 8a (paratype genitalia, B.M. slide 2485).

Holotype ♂ : " Mauritius, Réduit, .10.1950, *J. R. Williams* " " ex stems of *Cajanus cajan* " (genitalia, B.M. slide 2511).

Allotype ♀ : " Mauritius, Réduit, .6.1951, *J.R.W.*" " ex pods of *Canavalia ensiformis* ".

Paratypes : 6♀, 5♂, " Mauritius, Réduit, *J. R. Williams* " dated " .9.1950 ", " .10.1950 " and " .5.1951 " and bred from *Cajanus cajan* and *Canavalia ensiformis* ; 1♂, " Mauritius, Barkly, .11.1950, *J. R. Williams* " " ex Carob pods ".

Distribution : Mauritius, Madagascar.

Food-plants : *Cajanus cajan* (stems), *Canavalia ensiformis* (pods), carob (*Ceratonia siliqua*) (pods).

I have named this species after Mr. J. R. Williams whose investigations on behalf of the Department of Agriculture, Mauritius, helped towards its discovery.

Cryptophlebia rhynchias (Meyrick), new combination.

Platypeplus rhynchias Meyrick, 1905, J. Bombay nat. Hist. Soc., **16** p. 586.

Adult ♀ illustrated on Pl. XXIV, fig. 6.

Head, labial palpus, thorax and forewing light brown overlaid with purplish fuscous except towards termen ; elongate spot at termen brownish ochreous broadly edged with fuscous inwardly, a brownish ochreous suffusion at tornus delicately patterned with brownish fuscous, pretornal spot on dorsum triangular, blackish fuscous in middle, usually not very well defined, a minute but fairly conspicuous white speck in the discal cell. Cilia brownish with about seven broad brown lines unevenly spaced along the termen.

In the male, the forewing is not so strongly overlaid with purplish fuscous and the pretornal spot is practically obsolete.

Wing expanse, 12–29 mm.

Male genitalia, fig. 6.

Female genitalia, Pl. XXV, figs. 6 & 6a.

Distribution : S. India, Ceylon, Australia (Queensland), New Hebrides, Sudest I.

Food-plants : not known.

Cryptophlebia pallifimbriana, sp. n.

Adult ♀ illustrated on Pl. XXIV, fig. 5 (allotype).

Superficially similar to *rhynchias* but can be distinguished by the paler colour of the cilia.

Head, labial palpus, and thorax brownish. Forewing ochreous-brown, discal and basal areas with an irregular pattern of greyish and greyish-fuscous markings, elongate spot at termen below apex light ochreous suffused with golden brown except at edges and with four brownish lines arising from outer margin of this and running through cilia, innermost margin backed by a broad brownish-fuscous mark ; some light strigulations along costa ; a minute, not very conspicuous, white discal speck ; pretornal mark on dorsum brownish-fuscous, barred with fuscous across the middle. Cilia light ochreous-brown mixed with brown. Hindwing brownish-fuscous with a slight golden lustre ; cilia light ochreous becoming whitish at inner angle.

In the male, the general appearance and coloration of the forewing is somewhat lighter than in the female. In some examples of both sexes, there is a trace, more pronounced in the male, of a fairly broad, rich reddish-brown or brick-red fascia beginning at 1/3 on the dorsum but rarely discernible between the cell and the costa. The pretornal spot is poorly defined in the male and often represented by only a few fuscous scales.

Wing expanse, 19–33 mm.

Male genitalia, fig. 5.

Female genitalia, Pl. XXV, figs. 5 & 5a.

Holotype ♂ : " Fiji, Natoon [? Natovu], .4.1881, *R. Veitch* " (genitalia, B.M. slide 2545).

Allotype ♀ : " Fiji, Lautoka, 20.10.1927, *H. Phillips* ".

Paratypes : 2♀, " Fiji, Natoon [? Natovu], .4.1918, *R. Veitch,* larva on Ivi fruit [*Inocarpus edulis*]" and " Fiji, Lautoka, 20.10.27. *H. Phillips* ".

Distribution : Fiji, Tahiti, New Guinea, Vulcan I, Society Is., Marquesas, Austral Is., New Hebrides.

Food-plants : *Inocarpus edulis* is the only one known.

Cryptophlebia carpophagoides Clarke.

Cryptophlebia carpophagoides Clarke, 1951, J. Wash. Acad. Sci., **41** p. 299.

This is the only species of the genus *Cryptophlebia* recorded from the New World. The adult closely resembles *peltastica* superficially, and could easily be mistaken for that species.

Adults illustrated by J. F. G. Clarke (*l.c.*).

Only a few specimens of *carpophagoides* are known and only one of these, a female paratype, has been examined by the present author. The coloration of the forewing indicates that this species is probably slightly darker in appearance and more fuscous than *peltastica*, the forewing of the latter being browner. The labial palpus differs in these two species ; in *carpophagoides* it is gradually thickened and then slants off to conform to the line of the third segment, and in *peltastica* it is slender, abruptly broadened and truncate distally. The male of *carpophagoides* lacks the specialised sex-scaling of the hindwing which is found in *peltastica* and which is a conspicuous character of *ombrodelta* and *illepida*, and the tufting of the hind tibia is less pronounced than in *peltastica*.

Wing expanse, 20–24 mm.

Male genitalia, figured by J. F. G. Clarke (*l.c.*). The presence of small setae between the three very large setae in the margin of the valva distinguishes *carpophagoides* from *ombrodelta ;* in *peltastica*, small setae are present between the two large ones furthest from the base of the valva, *i.e.*, in the distal margin, but only a few very small, fine setae are found between the large ones in the ventral margin.

Female genitalia, figured by J. F. G. Clarke (*l.c.*). The signa are considerably smaller than those in *peltastica*, and the anterior edge of the eighth tergite is straight and not incurved as in *peltastica*.

Type in the U.S. National Museum.

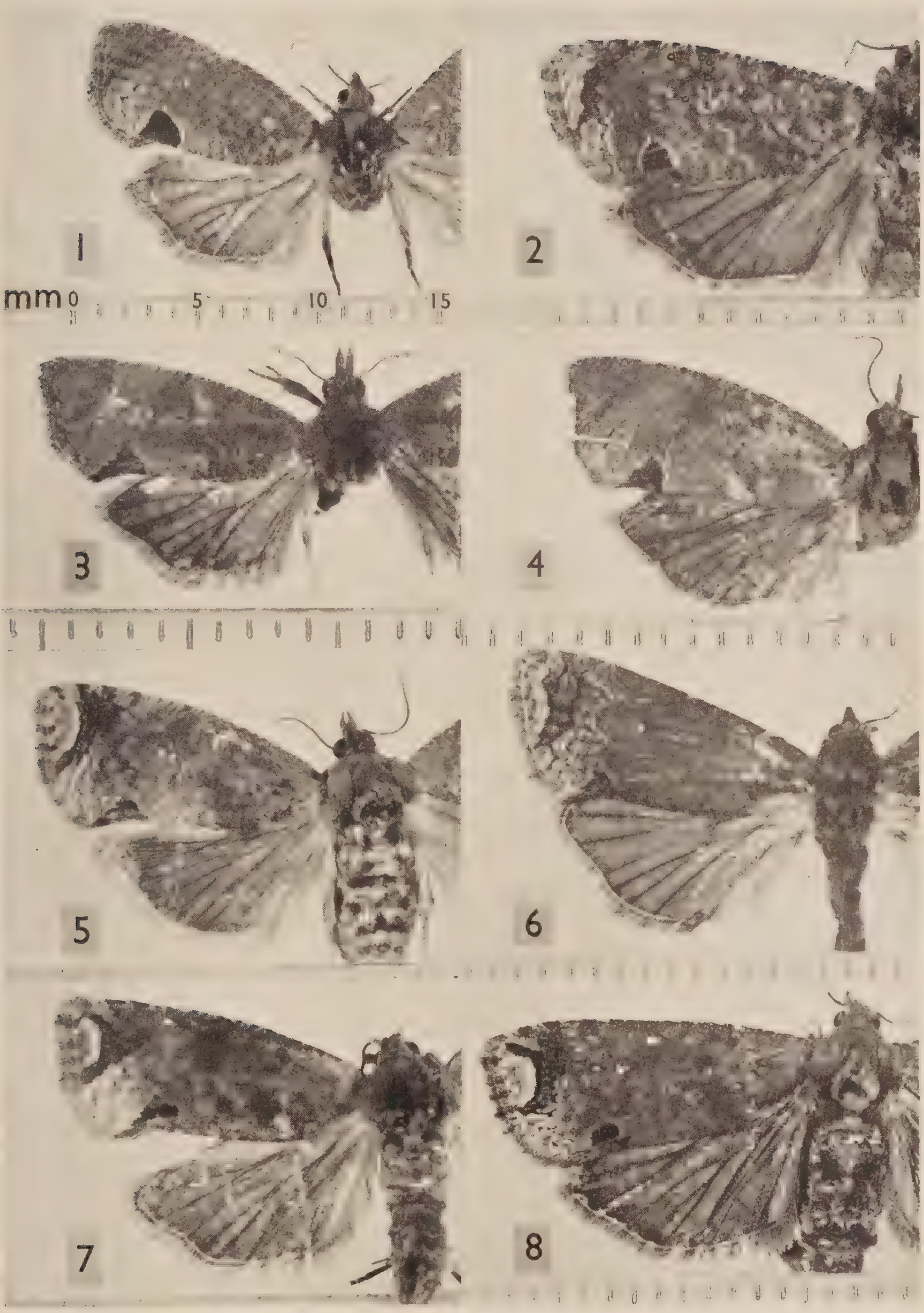
Distribution : Tucumán, Argentina.

Food-plants : " pacará " (seeds).

Summary.

This work was undertaken to unravel past confusion concerning the identity of certain economically important species of *Cryptophlebia*. It involved the study of several other species of the same genus and has resulted in the recognition of three new species and the transfer to *Cryptophlebia* of several species hitherto placed in other genera, mainly *Argyroploce*.

The three new species are described and 14 species are redescribed. The distribution of each is given and the food-plants are listed where known. The adult female and the male and female genitalia of each of the new species and certain others are illustrated.



Female examples of *Cryptophlebia* spp.

FIG. 1. *C. ombrodelta* Lower;
3. *C. illepida* Butler;
5. *C. pallifimbriana*, sp.n.;
7. *C. praesiliens* Meyrick;

FIG. 2. *C. peltastica* Meyrick;
4. *C. vitiensis*, sp.n.;
6. *C. rhynchias* Meyrick;
8. *C. williamsi*, sp.n.

THE LARVAE AND PUPAE OF SOME IMPORTANT LEPIDOPTERA.

By J. R. Williams, B.Sc., D.I.C., F.R.E.S.

Entomologist, Department of Agriculture, Mauritius.

The original intention of the author in planning this paper was to describe the immature forms of the three sugar-cane moth borers which are present in Mauritius. This plan has been extended to include also a few species which are closely allied to them.

The species which are described belong to the Agrotidae, Crambidae and Olethreutidae, and they are therefore treated separately in three sections.

The nomenclature used for the setae of the larvae is that of Hinton (1946). The larval descriptions were made from fully grown or nearly fully grown individuals. In all descriptions, the thoracic segments are designed by Roman numerals and the abdominal segments by Arabic numerals.

SECTION I.

This section deals with *Sesamia calamistis* Hamps., *S. inferens* (Wlk.) and *S. uniformis* Dudgn. Their larvae are stem-borers of several graminaceous plants, including sugar-cane, rice and maize. Only *S. calamistis* occurs in Mauritius, where its larva is known as the pink borer of sugar-cane. It has long been confused with *Speia vuteria* (Stoll) (see paper by Tams & Bowden in the present part of this *Bulletin*, pp. 647/666).

The following characters are common to *Sesamia calamistis* and *S. inferens*. (*S. uniformis* is not included as specimens of it have not been available; the species is briefly considered later from an existing description.)

Larva.—When mature, length about 30 mm., breadth about 3·5 mm. Colour: prothoracic shield light brown, dorsal surface of body a pronounced pink. Head (fig. 1 *a*) slightly broader than long, greatest width a little below middle of face. Clypeus well defined. Front (frons+clypeus) as high as wide, extending more than halfway to vertical triangle. Boundaries of adfrontals joining coronal suture at a point farther from vertical triangle than from front. Ocelli (fig. 1 *b*) six on each side, third and fourth close together. Mandibles (fig. 1 *c*) with five teeth, three of which are pointed. Labrum (fig. 1 *d*) with well defined epipharyngeal shield. Spinneret tapering towards apex, moderately long, extending a little beyond apex of distal seta of labial palp. Prolegs of equal size, crochets uniordinal in a mesoseries. Spiracles elongate oval, peritremes black. Body tubercles small and indistinct. Chaetotaxy: head (fig. 1 *ab*,) with C1 much shorter than C2. Setae AF1 and AF2 very small and close to adfrontal suture. Seta A2 directly behind A1 and very slightly above level of F1. Puncture Aa near to and mesad from A3. Puncture Va between V2 and V3, or occasionally a little laterad from a line joining them. Seta P1 level with AF2. Puncture Pb between P1 and P2, and close to the latter. Seta O2 much shorter than A3. Puncture Oa near ocellus 5. Seta SO2 anterolaterad from SO3. Puncture SOa near and below SO3. Body (fig. 1 *e–j*) with seta D2 postero-dorsad from D1 on 8, so that MD1 is well ventral to both. Seta SD1 absent on I, on II and 9 very slender, on 1–7 above spiracle, on 8 cephalad from spiracle and slightly anterior to SD2. Seta SD2 minute on abdomen, on 1 above level of spiracle, on 2–7 level with its upper (dorsal) margin, on 8 nearer level of its lower margin. Setae L2 and L3 absent on I, on 1–8 the three lateral setae are subequal; seta L1 almost as ventral as L2 on 7. Subventral (SV) group unisetose

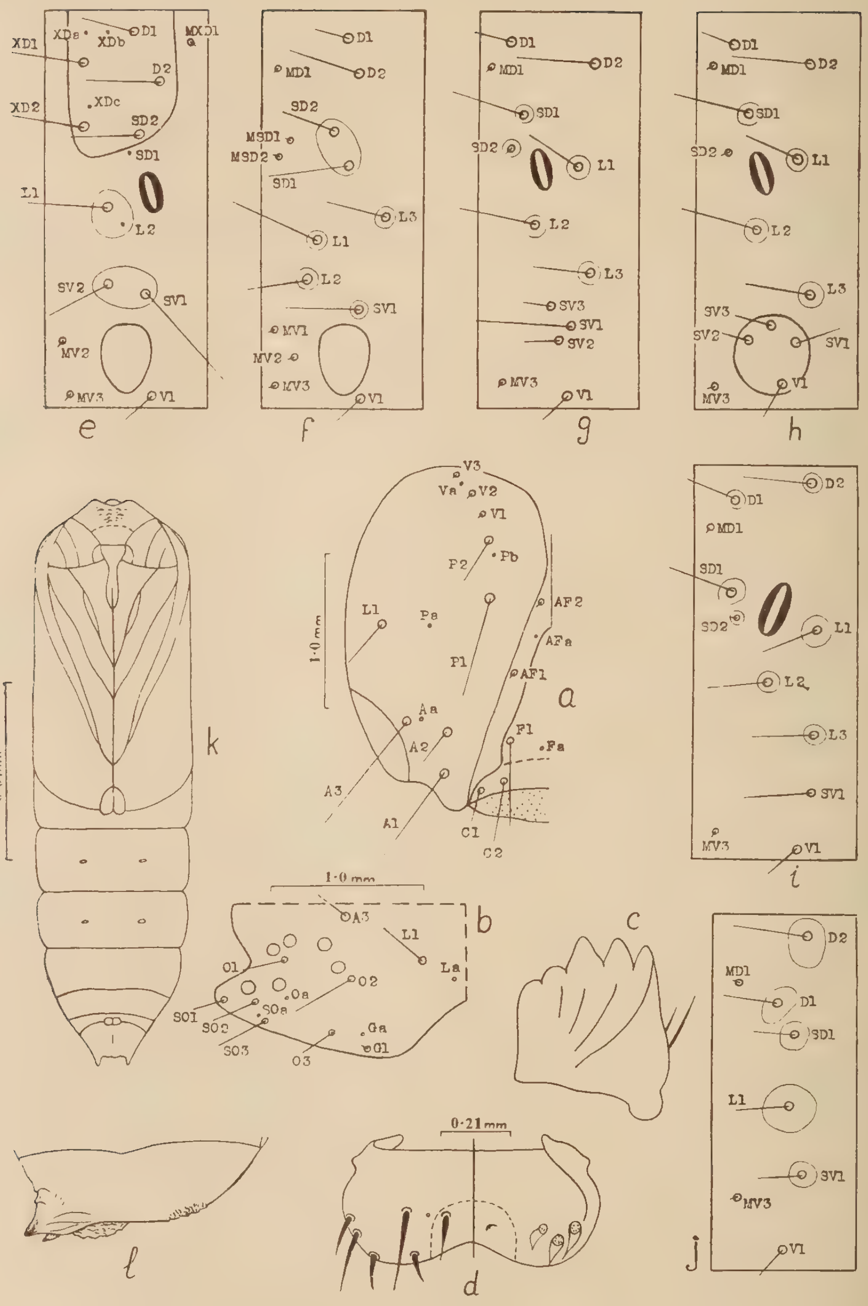

XD1
XDa
XDb
D1
MXD1
D2
XD2
XDc
SD2
SD1
L1
L2
SV2
SV1
MV2
MV3
V1
e
MD1
MSD1
MSD2
L3
MV1
f
SV3
g
h
i
j
V3
Va
V2
Pb
P2
Pa
P1
AF2
AFa
AF1
1·0 mm
Aa
A2
A3
A1
F1
Fa
C1
C2
a
k
6·0 mm
A3
La
b
O1
O2
Oa
SOa
SO1
SO2
SO3
O3
Ga
G1
c
0·21 mm
d
l

Fig. 1.—*Sesamia calamistis* Hamps. Mature larva—(*a*) head from face view; (*b*) ocellar area of head; (*c*) mandible; (*d*) labrum, with epipharyngeal surface on right; (*e–j*) setal maps of segments I, II, 2, 6, 8, and 9 respectively. Pupa—(*k*) ventral surface; (*l*) cremaster.

on II, III, 7, 8, and 9 ; bisetose on I and 1 ; trisetose on 2–6. Microscopic MD group bisetose on III. No secondary setae.

Pupa (fig. 1 *k*).—Length usually about 17 mm., breadth about 4 mm. Head dark reddish brown. Thorax and abdomen reddish brown dorsally, yellowish brown ventrally. Vertex reduced to two triangular pieces. Front roughly corrugated, and bearing an apical tubercle. Frons : clypeal suture, pilifers and genae distinct. Maxillary palps not evident. Labial palps elongated between maxillae. Femora of I exposed. Legs of II not reaching eyepieces anteriorly nor wingtips posteriorly. Legs of III extending to, or almost to, wingtips. Spiracles of II slit-like, elongated, prominent. Segments 1–8 with numerous round and oval pits, each being a shallow depression with a thickened rim; they are more numerous dorsally. Cremaster present.

S. calamistis Hamps.

Larva.—Head very dark brown, its integument wrinkled. On 8, the angle formed by lines through D1 and D2 of each side (fig. 2 *b*) averages 25° (measured on eight specimens—max. angle 45°, min. angle 12°). On I, the missing setae SD1 and L2 are represented by easily detectable punctures (fig. 1 *e*).

Pupa.—Frontal tubercle possessing prominently raised cornicles. Abdominal pits on 4, 5, 6 and 7 dense near cephalic margin dorsally. Cremaster (fig. 1 *l*) with two dorsal spines and a ventral tubercled protuberance.

S. inferens (Wlk.).

A very brief description of the larva has been given by Isaac and Rao (1941), while Gardner (1948) describes it sufficiently to enable him to place the genus in his grouping of Indian Agrotid larvae. A good description of the pupa has been given by Isaac and Venkatraman (1941).

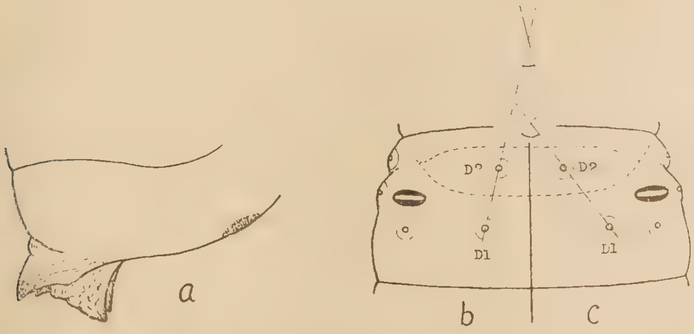


Fig. 2.—(*a*) cremaster of *Sesamia inferens* (Wlk.) ; (*b*) angle formed on segment 8 by dorsal setae of *S. calamistis* Hamps. ; (*c*) same of *S. inferens.*

The characters described below, which distinguish the species from *calamistis*, were determined by the examination of ten larvae and two female pupae obtained from India through the kindness of Dr. S. L. Hora of the Zoological Survey of India.

Larva.—Head light brown, smooth or nearly so. On 8, the angle formed by lines through D1 and D2 of both sides (fig. 2 *c*) averages 80° (measured on eight specimens—max. angle 88°, min. angle 72°). On I, missing seta L2 represented by an extremely minute puncture which is difficult to detect. No puncture found representing SD1.

Pupa.—Frontal tubercle without prominently raised cornicles, but with two nostril-like indentations. Abdominal pits on 4, 5, 6 and 7 less concentrated near cephalic dorsal margin. Cremaster (fig. 2 *a*) with two dorsal spines and with a ventral lobe which is developed into a ridge with a spine at each end.

S. uniformis Dudgn.

This is another Indian species. Specimens were not available for study but the pupa is described by Isaac and Venkatraman (1941) as similar to *inferens* except for the cremaster which has four spines on its ventral lobe.

Remarks.

(1) The absence of setae SD1 and L2 on the prothorax of *S. calamistis* and *S. inferens* is worthy of comment, for Hinton (1946), in his comprehensive study of the setae of Lepidopterous larvae, states that both are primary setae on that segment. The term "primary", when applied in its generally accepted sense to setae of Lepidopterous larvae, implies setae which are present on all instars of all groups, excepting a few specialised groups in which some of them may be lost after the first instar, or alternatively may only appear after the first instar. Again, in forms where secondary setae are present in the first instar, the primary setae may be indistinguishable. *S. calamistis* fits none of these exceptional cases, for it was found that the two setae are represented by punctures in the first instar as well as in the subsequent ones. Presumably both setae are also absent on I in the first instar of *S. inferens*, but unfortunately no larvae in the first instar have been available for examination.

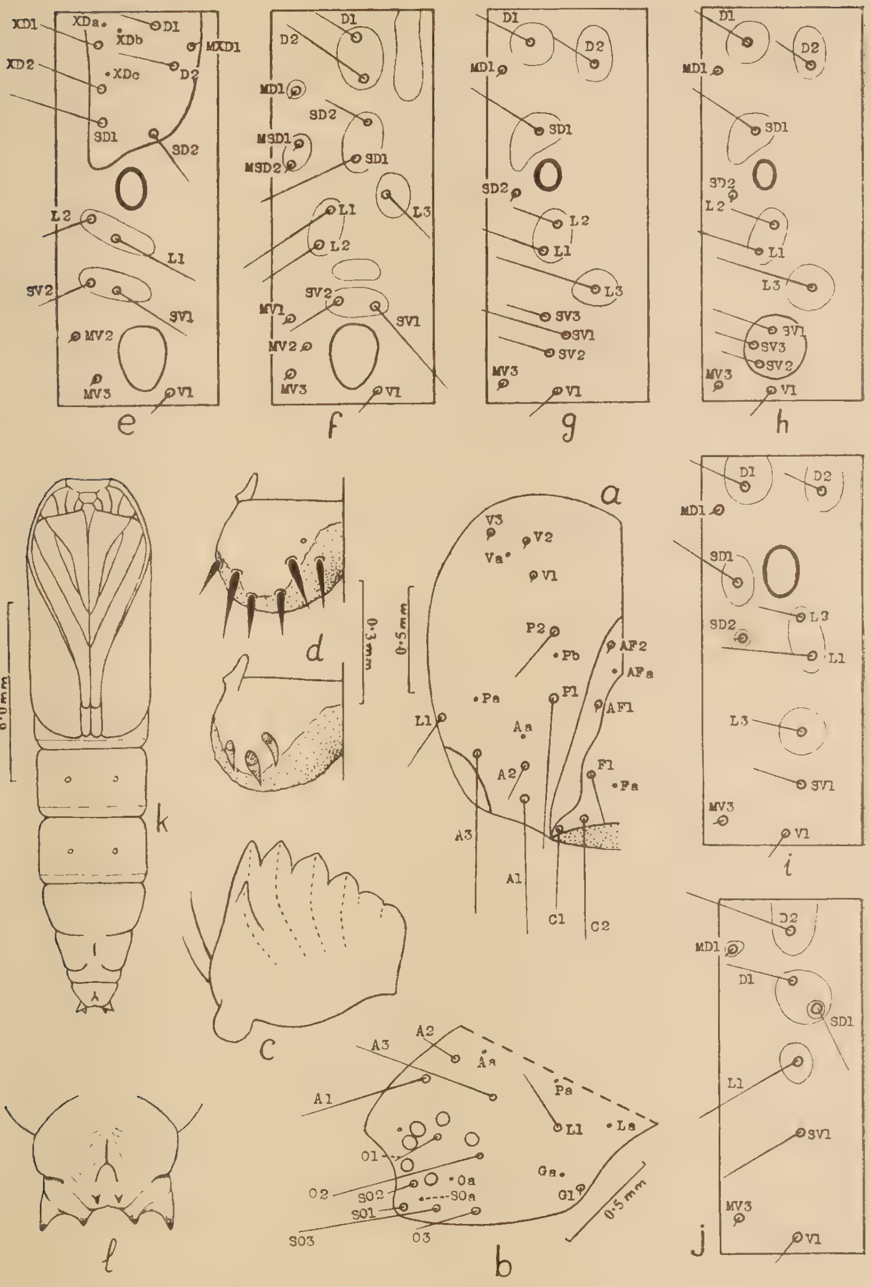
(2) Gardner (1948), when describing the larva of *S. inferens*, states that SD1 on 8 is anterior to the spiracle and slightly above its level. This is undoubtedly an error, for with all larvae of both species which have been examined, the seta is clearly within the level of the spiracle, that is, cephalad from it.

SECTION II.

Two Crambid sugar-cane borers of the Old World, *Proceras sacchariphagus* Bojer and *P. indicus* Kapur, are considered in this section. They have been known under a variety of names, and for these reference is made to Kapur (1950). *P. sacchariphagus* is the spotted borer of sugar-cane in Mauritius, while *P. indicus* is the Indian species which has often been referred to as *Diatraea venosata* (Wlk.).

Larvae of *P. indicus* (ten specimens) were supplied by Dr. S. L. Hora of the Zoological Survey of India, but no pupae were obtained. The following larval characters are common to both species.

Larvae.—When mature, length about 30 mm., breadth about 4 mm. Colour: Head brown. Prothoracic shield light brown with darker areas laterally and along posterior margin. Body white, with brown or black tubercles. The pigmentation of any tubercle is more or less directly proportional to its proximity to the mid-dorsal line. Two longitudinal violet stripes on each side, one coinciding with the line of the spiracles, the other with the tubercles of the dorsal setae. There is individual variation regarding the distinctness of the stripes and the degree of tubercular pigmentation. Head (fig. 3 *a*) slightly broader than long, greatest width above middle of face. Clypeus indistinct. Front (frons + clypeus) longer than wide, extending half-way to vertical triangle. Boundaries of adfrontals joining coronal suture at a point 1½ times as far from vertical triangle as from front. Ocelli (fig. 3 *b*): six on each side, third aud fourth contiguous. Mandibles (fig. 3 *c*) with six teeth, four of which are pointed; there is a sharp point at the base of the outer tooth. Labrum (fig. 3 *d*) with median incision varying from acute to moderately


XD1
XDa
XDb
D1
MXD1
XD2
XDc
D2
SD1
SD2
L2
L1
SV2
SV1
MV2
MV3
V1
e
D1
D2
MD1
SD2
MSD1
MSD2
SD1
L1
L3
L2
SV2
MV1
SV1
MV2
MV3
V1
f
D1
D2
MD1
SD1
SD2
L2
L1
L3
SV3
SV1
SV2
MV3
V1
g
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D2
MD1
SD1
SD2
L2
L1
L3
SV1
SV3
SV2
MV3
V1
h
6·0mm
k
d
0·3mm
c
a
V3
V2
Va
V1
0·5mm
P2
Pb
AF2
AFa
Pa
P1
AF1
L1
Aa
A2
F1
Fa
A3
A1
C1
C2
D1
D2
MD1
SD1
SD2
L3
L1
L3
SV1
MV3
V1
i
D2
MD1
D1
SD1
L1
SV1
MV3
V1
j
l
A2
A3
Aa
A1
Pa
L1
La
O1
Oa
O2
SO2
SOa
SO1
Ga
G1
0·5mm
SO3
O3
b

Fig. 3.—*Proceras sacchariphagus* Boj. Mature larva—(*a*) head from face view; (*b*) ocellar area of head; (*c*) mandible; (*d*) labrum, epipharyngeal surface below; (*e–j*) setal maps of segments I, II, 2, 6, 8, and 9 respectively. Pupa—(*k*) ventral surface; (*l*) cremaster.

concave; epipharyngeal shield not sharply defined. Prolegs of equal size, crochets in a uniserial circle and decreasing in size externally (laterally); triordinal, internally at least. Spiracles of I and 8 larger than remainder and of about equal size; those of 8 dorsal to line of other spiracles. Chaetotaxy: head (fig. 3 *a*, *b*) with F1 shorter than clypeal setae. Puncture Fa mesad from and well below F1. Setae AF1 and AF2 minute. Distance between F1 and AF1, and between AF1 and AF2 about equal. Puncture AFa nearer AF2 than AF1, and below and mesad from the former. Seta A2 directly behind A1; distance between A2 and A3 clearly greater than that between A1 and A2. Puncture Aa above A2, sometimes above and slightly laterad from it. The three anterior setae form an angle of 90° approximately. Seta O1 about $1\frac{1}{2}$ times as long as A2, close to and equidistant from ocelli 2 and 3. Vertical (V) setae forming an obtuse angle with Va on, or slightly laterad from, a line joining V1 and V3. Body (fig. 3 *e–j*) with tubercles of D1 rounded, and those of D2 oval on 1–7. Seta D1 longer than D2 on 1–8, *vice versa* on 9. Seta SD1 dorsad and slightly cephalad from spiracle on 1–7, cephalad from spiracle on 8. On 9, SD1 posteroventrad from D1 and on the same tubercle; it is a slender seta with a thickened socket. Seta SD2 minute on abdomen, and antero-ventrad from spiracle on 8. Seta L3 not present on I; seta L1 is the longest of the lateral setae on 8, being ventrad and slightly caudad from L2. Subventral (SV) group unisetose on 8 and 9, bisetose on I, II, III, and 7, trisetose on 1–6. Seta SV3 antero-dorsad from SV1 on 1 and 2, antero-ventrad from SV1 on 3–6 although not as ventrad as SV2. Seta SV2 cephalad and slightly dorsad from SV1 on 7. No secondary setae.

P. sacchariphagus Bojer

Larva.—Spiracles rounded, but with vertical diameter greater than horizontal; peritreme of more or less uniform thickness in all its circumference. Distance between Aa and A2 usually about equal to, or a little greater than, that between A1 and A2. Tubercles of setae D2 of the same segment only very slightly further apart than those of D1 on 1–7. On 9, D1 and SD1 on a common tubercle; setae D2 on a common dorsal tubercle; MD1 distinct from these tubercles (fig. 3 *j*). Seta SD2 on 2–7 anterior to spiracle and slightly below its level, or level with its lower margin (fig. 3 *g*, *h*).

Pupa (fig. 3 *k*).—♀♀ 16–20 mm. long, 3·5–4 mm. wide (10 specimens); ♂♂ 13–16 mm. long, 2·5 mm. wide (10 specimens). Reddish brown, darker dorsally. Body tapering after 6. Front slightly concave, or straight, at extremity of head when viewed from above or below. Clypeo–labral suture, pilifers, maxillary palps, labrum, and labial palps distinct. Tentorial invaginations well marked. Maxillae less than half length of wings. Wings extending over about $\frac{3}{4}$ of 4. Femora of I visible. Legs of II not usually extending to wingtips. Spiracles elongate-oval, prominent. Segments 1–7 with chitinised rugosity on cephalic halves which is more pronounced dorsally, especially on 4–7; on 5, 6 and 7 the rugosity encircles the body. Flexible caudal areas of abdominal segments with minute polygonous chitinised areas. Caudal halves of 1–7 with dorsal band of microscopic spines which extends ventrally to proleg scars on 5 and 6. Anus Y-shaped. Cremaster (fig. 3 *l*) with lateral grooves, and consisting of two lobes each bifurcating into two spines, an inner and an outer, the latter usually being the larger. A third pair of small spines is sometimes present between the lobes.

P. indicus Kapur

Previous descriptions of the larva are those of Gupta (1940) and Isaac and Rao (1941). Neither is adequate.

Larva.—Spiracles broadly oval, with peritreme thinner dorsally and ventrally. Distance between Aa and A2 about half that between A1 and A2. Tubercles of setae D2 of the same segment about twice as far apart as those of D1 on 1–7. On 9, setae

D1, D2, SD1, and MD1 of both sides on one large tubercle. Seta SD2 cephalad from spiracle on 2–7. Segments 1–7 with a tubercle, which possesses no seta, caudad from spiracle.

The pupa has been described by Gupta (*l.c.*) and by Isaac and Venkatraman (1941). The latter author's description of it is detailed, but does not include a character which would serve to distinguish it from the pupa of *P. sacchariphagus*.

SECTION III.

Meyrick (1930) described *Argyroploce socratica* and *A. symmictopa* from specimens collected in Mauritius, and in the same paper recorded *A. peltastica* Meyr., *A. leucotreta* Meyr. and *A. schistaceana* (Snell.) from the island. The latter is well known as a borer of sugar-cane tillers, and in the course of the present work, an attempt was made to collect the larvae and pupae of all these species for description. However, *A. socratica* and *A. symmictopa* were not found. They were described from single specimens reared from *Tamarindus indica* and " herbe-à-mèche ", respectively ; it has not been possible to discover the identity of the latter plant.

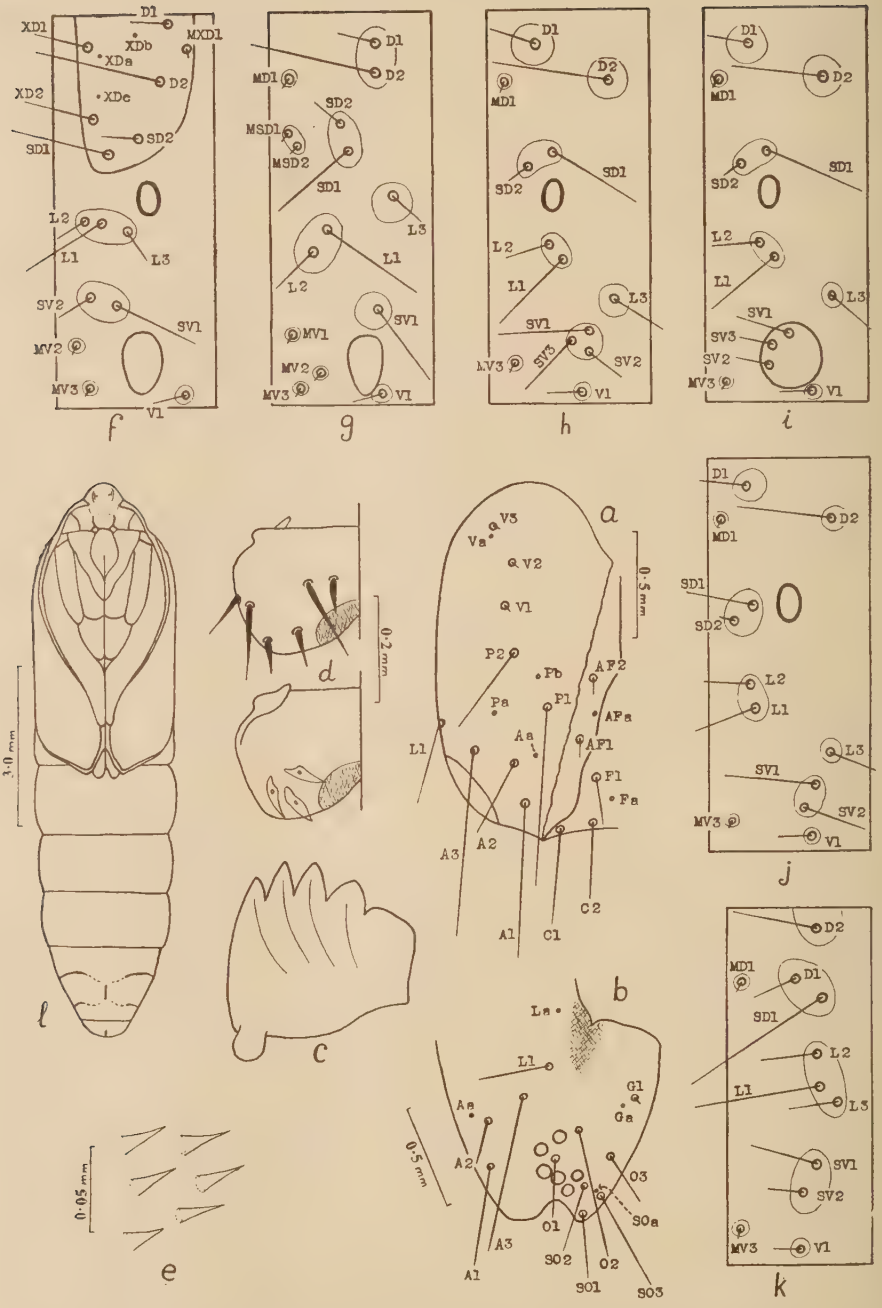
Mr. J. D. Bradley of the British Museum, in the preceding paper published in the present issue of this *Bulletin* (p. 682), places *peltastica* in the genus *Cryptophlebia* and confirms that this species, which was described from South Africa, occurs in Mauritius. He also describes a new species from the island as *C. williamsi*. Previous misidentification of material from Mauritius has resulted in published records from there of *Argyroploce rhynchias* (Meyr.) and *A. illepida* (Butl.), neither of which actually occurs there. Bradley's work has shown that the specimens thus determined are referable to *C. williamsi* and *C. peltastica*, respectively.

Adult specimens of the four species, *schistaceana*, *leucotreta*, *williamsi* and *peltastica*, of which the larvae and pupae are described hereafter, have been deposited, after identification by Mr. Bradley, in the British Museum and are available there for reference.

These four species are important pests in Mauritius. *A. schistaceana*, as already mentioned, is a borer of sugar-cane tillers. *A. leucotreta* is a common borer of peach fruits in Mauritius and has also been reared from castor seeds there (coll. L. A. Moutia); in Africa, it is well known as a pest of *Citrus* fruits and cotton bolls as well as peaches. *C. peltastica* was recorded by Meyrick (*l.c.*) from the bean, *Canavalia ensiformis* ; the present author has reared it from fruits of the litchi (*Litchi chinensis*), stems of the flamboyant (*Poinciana regia*), and pods of carob (*Ceratonia siliqua*) and *Tamarindus indica*. *C. williamsi* has been reared by the author from both stems and pods of *Canavalia ensiformis* and also from stems of *Cajanus cajan* and pods of carob.

The following characters are common to *Argyroploce schistaceana*, *A. leucotreta*, *Cryptophlebia peltastica* and *C. williamsi*.

Larva.—Colour : head brown, with mottled appearance under magnification ; patch of deeper pigmentation laterally at posterior margin (fig. 4 *b*). Head (fig. 4 *a*) trapezoidal from face view. Vertical triangle very deep. Boundaries of adfrontals reaching vertical triangle. Clypeus poorly defined. Front (frons+clypeus) as high as wide. Ocelli (fig. 4 *b*) six on each side, third and fourth approximate, sixth below fourth and fifth and about equidistant from them. Mandibles (fig. 4 *c*) with four sharp teeth and an inner rounded cutting edge. Labrum (fig. 4 *d*) with epipharyngeal shield sharply defined. Prolegs with crochets in a biordinal uniserial circle. Body invested with minute spines (figs. 4 *e* & 5). Chaetotaxy : head (fig. 4 *a*, *b*) with vertical setae very forward on face, forming either a straight line, or a very obtuse angle pointing to median line ; seta V2 equidistant from V1 and V3. Seta P2 above and laterad from P1. Anterior setae forming an angle much greater than 90°; puncture Aa above and mesad from A2, but sometimes below and mesad. Puncture Fa below


D1
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XDb
MXD1
XDa
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XD2
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L1
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k
0·05 mm
e

Fig. 4.—*Argyroploce schistaceana* (Snell.). Mature larva—(*a*) head from face view; (*b*) ocellar area of head; (*c*) mandible; (*d*) labrum, epipharyngeal surface below; (*e*) body spines; (*f–k*) setal maps of segments I, II, 2, 6, 8, and 9 respectively. Pupa—(*l*) ventral surface.

and mesad from F1. Subocellar setae forming a right angle, similarly with SO3, SO2, and O3. Puncture SOa between SO2 and SO3. Puncture Oa not found. Body (fig. 4 *f–k*) with SD1 antero-ventrad from SD2 on I, directly above spiracle on 1–7. Lateral group trisetose on I–9, on 1–7 L1 and L2 placed obliquely, L1 being postero-ventrad from L2. Seta L1 either the same length as L3, or longer than it, on all abdominal segments. Subventral group unisetose on II and III, bisetose on I and 8, trisetose on 1–6. No secondary setae.

Pupa (fig. 4 *l*).—Reddish brown. Body tapering after 4. Front raised. Clypeo-labral suture easily discernible. Pilifers, maxillary palps, labrum, and tentorial invaginations distinct. Labial palps large. Maxillae short. Wings of III visible. Wings extending over varying distance over 4. Coxae of I, II, and III visible. Legs of II not reaching eyepieces anteriorly or wingtips posteriorly. Abdominal spiracles broadly oval. Proleg scars not visible. Segment 1 without spines, 3, 4, 5, 6, and 7 with two dorsal rows of stout spines, a single dorsal row on 8 and 9. Cremaster absent.

A. schistaceana (Snell.).

Larva.—When mature, length about 25 mm., breadth about 3 mm. Colour : head moderately dark brown ; body dirty white, tubercles pigmented but too small to give spotted appearance. Head as long as wide. Ocelli 3 and 4 almost contiguous. Spiracles broadly oval. Body with spines as in fig. 4 *e*. Chaetotaxy : head (fig. 4 *a*, *b*) with puncture Va near V3. Puncture Pb equidistant from P1 and P2. Anterior setae equidistant. Puncture AFa about equidistant from AF1 and AF2. Body (fig. 4 *f–k*) with puncture XDa postero-ventrad from XD1. Seta D1 on I posterior to D2 and above level of XD1. Setae SD1 and SD2 with common tubercle on abdominal segments ; SD1 on 8 cephalad from spiracle. Seta L1 longer than L3 on abdomen, on 8 it is almost directly ventrad from L2. Subventral group trisetose on 7, bisetose on 9. On 1 and 2, SV2 ventrad from SV1, SV3 antero-ventrad from SV1. Tubercle of ventral seta in contact with coxa on II and III.

Pupa (fig. 4 *l*).—9–12 mm. long, 2–3 mm. wide (2♀♀, 2♂♂). Front very prominently raised, with depression on its ventral face. Dorsum of II with transverse striations, without punctures. Legs of III extending beyond wingtips. Single row of dorsal spines on 2. Segment 10 without spines, but with long hooked setae arranged roughly in a transverse row.

A. leucotreta Meyr.

(A previous description of the larva is that of Stofberg (1948).)

Larva.—When mature, length about 15 mm., breadth about 2·5 mm. Colour : head rather light brown ; body pale with reddish hue, tubercles without, or with faint, pigmentation. Head wider than long. Ocelli 3 and 4 very close together. Spiracles round. Body with spines as in fig. 5 *a*. Anal comb present. Chaetotaxy : head with puncture Va between and equidistant from V2 and V3. Puncture Pb nearer P2 than P1. Seta P2 nearer A1 than A3. Puncture AFa much nearer AF2 than AF1. Body with puncture XDa postero-ventrad from XD1. Seta D1 on I slightly posterior to D2 and slightly below the level of XD1. Setae SD1 and SD2 with common tubercle on abdominal segments, SD1 on 8 antero-ventrad from spiracle. Setae L1 and L3 subequal on abdomen, on 8 L1 postero-ventrad from L2 as on 1–7. Subventral group bisetose on 7, unisetose on 9. On 1 and 2 SV2 ventrad and slightly cephalad from SV1, SV3 antero-dorsad from SV1. Tubercle of ventral seta not in contact with coxa on II and III.

Pupa.—8–10 mm. long, 2–2·5 mm. wide (3♀♀, 5♂♂). Front raised, without depression on its ventral face. Dorsum of II heavily punctured. Legs of III extending to, but not beyond wingtips. Two rows of dorsal spines on 2. Spines on 8 and 9 very well developed. Segment 10 with spines and with two pairs of hooked setae.

Cryptophlebia williamsi Bradley

Larva.—When mature, length about 25 mm., breadth about 3·5 mm. Colour : head dark brown ; body with reddish hue which is often pronounced, and with large, deeply pigmented tubercles giving a spotted appearance. Head wider than long. Ocelli 3 and 4 widely separated, but closer together than the others. Spiracles broadly oval. Body with spines as in fig. 5 *b*. Chaetotaxy : head with puncture Va between V2 and V3 and usually slightly nearer the former. Puncture Pb near P2. Anterior setae about equidistant. Puncture AFa much nearer AF2 than AF1. Body with puncture XDa postero-dorsad from XD1. Seta D1 on I directly above D2, and slightly above the level of XD1. Setae SD1 and SD2 with common tubercle on abdominal segments, SD1 on 8 anterad and slightly ventrad from spiracle. Setae L1 and L3 subequal on abdomen, on 8 L1 caudad from L2. Subventral group trisetose on 7, unisetose on 9. On 1 and 2 SV2 ventrad and slightly cephalad from SV1, SV3 antero-dorsad from SV1. Tubercle of ventral seta quite separate from coxa on II and III.

Pupa.—10–16 mm. long, 3–3·5 mm. wide (3♀♀, 3♂♂). Spines on 8 and 9 developed, but less so than in *A. leucotreta.* Dorsum of II heavily and coarsely punctured. Segment 10 with two pairs of hooked setae and with spines, two of which (one on each side of the anus) are stout and hooked. Otherwise as *A. leucotreta.*

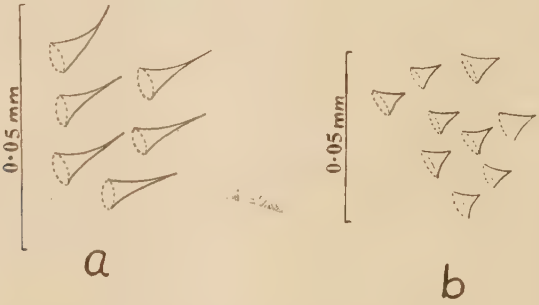

Fig. 5.—(*a*) body spines of *Argyroploce leucotreta* Meyr. ; (*b*), same of *Cryptophlebia williamsi* Bradley and *C. peltastica* (Meyr.).

C. peltastica (Meyr.)

Stofberg (1948) describes the subventral setae on segments 7 and 9 to distinguish the larva from that of *A. leucotreta.*

Larva.—As *williamsi* except as follows. When mature, length about 20 mm., breadth about 3 mm. Body with tubercles slightly smaller, and lightly pigmented so that spotting is not pronounced. Setae SD1 and SD2 with common tubercle on 1, on 2–8 SD2 with its own small tubercle which is occasionally confluent (especially on 8) with the SD1 tubercle. Seta L1 on 8 postero-ventrad from L2 as on 1–7. Subventral group bisetose on 9.

Pupa.—Indistinguishable from that of *williamsi.*

The larvae of these four Olethreutids are readily distinguished as follows.

1. Anal comb absent..2
   Anal comb present...*A. leucotreta*

2. SV setal group bisetose on 9 3
   SV setal group unisetose on 9 .... *C. williamsi*
3. Setae SD1 and SD2 with separate tubercles on 2–8 .... *C. peltastica*
   Setae SD1 and SD2 with a common tubercle on 2–8 .... *A. schistaceana*

Summary.

The larvae and pupae of the following Lepidoptera, all of which are of economic importance in Mauritius and most of them elsewhere also, are described :—

The Agrotids, *Sesamia calamistis* Hamps. and *S. inferens* (Wlk.) ; the Crambids, *Proceras sacchariphagus* Boj. and *P. indicus* Kapur (larva only) ; and the Olethreutids, *Argyroploce schistaceana* (Snell.), *A. leucotreta* Meyr., *Cryptophlebia peltastica* (Meyr.) and *C. williamsi* Bradley.

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SEASONAL VARIATIONS IN THE MEAN SIZE OF TSETSE FLIES.

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The tsetse flies here considered are non-teneral males from untouched control areas about Shinyanga, Tanganyika Territory ; Block 9 near Shinyanga for *Glossina swynnertoni* Aust. and *G. pallidipes* Aust., and Mkwemi (Kahama District) for *G. morsitans* Westw.

The size of the individual offspring is laid down at birth (Mellanby, 1936) and is unaffected by conditions during pupal life. Size is herein assessed by measuring the middle part of the fourth longitudinal vein in the wing (Jackson, 1945). The mean age of non-teneral male flies measured, judged by the wear on their wings (Jackson, 1946, 1948, 1950), is apparently some 3–4 weeks ; and as the pupal period is about 35 days for males at mean Shinyanga temperatures (23°C.) we should expect the size of the flies to be determined at an average of 2 months before they are collected for measurement, normally about the middle of each month. A correlation might therefore be expected between mean vein measurement for any month and the mean environmental conditions of the last month but one.

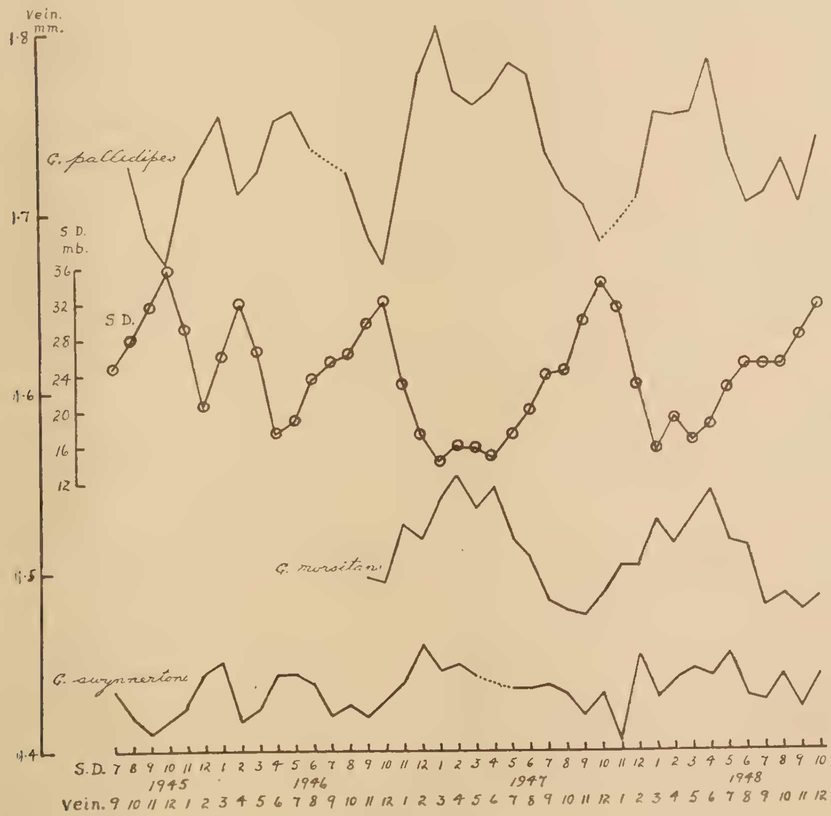

Fig. 1.

TABLE I.

Mean vein lengths and saturation deficits.

Month	1	2	3	4	5	6	7	8	9	10	11	12
G. pallidipes : mean vein length, mm.												
1945 ...	—	—	—	—	—	—	—	—	—	1·727	1·689	1·673
1946 ...	1·720	1·737	1·755	1·711	1·723	1·752	1·757	1·737	—	1·723	1·691	1·671
1947 ...	1·728	1·770	1·804	1·767	1·760	1·767	1·783	1·777	1·734	1·714	1·705	1·684
1948 ...	—	1·717	1·755	1·753	1·755	1·785	1·734	1·705	1·710	1·729	1·705	1·738
G. morsitans : mean vein length, mm.												
1946 ...	—	—	—	—	—	—	—	—	—	—	1·497	1·494
1947 ...	1·526	1·518	1·538	1·552	1·535	1·547	1·518	1·507	1·484	1·478	1·475	1·487
1948 ...	1·503	1·503	1·528	1·515	1·530	1·545	1·517	1·514	1·480	1·486	1·477	1·482
G. swynnertoni : mean vein length, mm.												
1945 ...	—	—	—	—	—	—	—	—	1·434	1·419	1·411	1·418
1946 ...	1·425	1·443	1·450	1·417	1·424	1·443	1·443	1·438	1·420	1·426	1·419	1·428
1947 ...	1·437	1·459	1·445	1·448	1·442	—	1·435	1·435	1·437	1·432	1·420	1·431
1948 ...	1·405	1·452	1·429	1·440	1·445	1·442	1·454	1·430	1·428	1·442	1·423	1·439
Mean saturation deficit, 2 p.m., mb.												
1945 ...	18	18	25	24	19	21	25	28	32	36	29	20
1946 ...	26	32	27	17	19	24	25	26	30	32	23	17
1947 ...	14	16	16	15	17	20	24	24	30	34	31	23
1948 ...	15	19	17	18	22	25	25	25	28	31	27	22
G. pallidipes, numbers measured												
1945 ...	—	—	—	—	—	—	—	—	—	8	14	8
1946 ...	32	11	11	41	55	59	33	12	—	16	4	16
1947 ...	10	20	50	27	20	7	13	14	15	10	7	4
1948 ...	7	5	11	21	11	4	4	3	7	6	8	4
G. morsitans, numbers measured												
1946 ...	—	—	—	—	—	—	—	—	—	—	45	96
1947 ...	34	58	86	46	34	42	21	41	50	50	9	28
1948 ...	44	50	28	12	18	54	28	47	47	50	50	52
G. swynnertoni, numbers measured												
1945 ...	—	—	—	—	—	—	—	—	15	221	108	89
1946 ...	98	102	52	301	201	178	247	89	58	98	68	50
1947 ...	50	50	50	50	50	—	37	51	67	50	50	50
1948 ...	22	35	30	32	51	39	31	48	88	24	25	41

Examination of the data shows (fig. 1) a negative correlation of the mean vein length with the 2 p.m. mean saturation deficit of 2 months before. This correlation is strongest for *G. pallidipes*, which for the period October 1945 to December 1948 (lacking data for September 1946 and January 1948) gives the remarkably high coefficient of −0·90. (After 1948 the numbers are too low.) The corresponding correlation coefficient with maximum temperature is lower, −0·79 ; the probability of this difference occurring by chance with 37 months of observations is about 1 in 12.

This difference between the two correlations is thus not significant ; if it were real it would mean that the size of the offspring is determined not merely by a direct temperature effect acting on the mother flies (Buxton & Lewis, 1934) but also in part at least by desiccation, probably causing seasonal malnutrition of the mothers.

For *G. swynnertoni* over the same period (October 1945 to December 1948) there are available 38 months, with June 1947 missing ; the correlation with 2 p.m. saturation deficit is −0·68, significantly lower than for *G. pallidipes*.

The amplitude of the response in size of *G. swynnertoni* to season is also less pronounced than that of *G. pallidipes*, and we might possibly therefore expect the lower correlation just obtained. Thus for the period October 1945 to December 1948, the coefficient of variation for the monthly means of *G. pallidipes* veins is 2·54 per cent., compared with only 0·88 per cent. for *G. swynnertoni*, implying that *G. pallidipes* is about three times more responsive to seasonal changes in its environment. My colleague, Mr. W. H. Potts, suggests that this may imply that *G. pallidipes* is less at home in Shinyanga than is *G. swynnertoni*, and he is supported by the spontaneous collapse of *G. pallidipes* in some of our observational blocks. It is true that the numbers of *G. pallidipes* measured each month (Table I) were less than those of the other two species, but a glance at the graph (fig. 1) shows that their great variation is seasonal and not erratic.

Data for *G. morsitans* are available continuously from November 1946 to December 1948. For these 26 months, the correlation coefficient of mean monthly vein length with 2 p.m. saturation deficit at Shinyanga of 2 months before is −0·81, and the coefficient of monthly mean variation is 1·53 per cent. Both these are intermediate between the values for the other two species : the degree of seasonal variation, and its dependence on saturation deficit, are both less marked than in *G. pallidipes* and more marked than in *G. swynnertoni*. Probably the correlation coefficient might have been higher had the meteorological data been obtained nearer to where the *G. morsitans* were caught, instead of nearly 100 miles away.

I have also compared the data for *G. pallidipes* allowing the 2 months' lag in saturation deficit with the same data allowing only 1 month's lag, and again with no lag at all. The result is quite decisive : with 2 months' lag the correlation coefficient is 0·90, with 1 month's lag it is only −0·32, and with no lag at all it is smaller still, 0·24. There are 37 pairs of observations in each case, so there is no doubt of the advantage of the 2-month lag over the other arrangements.

In working out these data I have borne in mind the warning by Moran (1949), who explains that for accurate tests of significance by the usual methods the individual values must not be serially correlated, as these obviously are ; and he gives a formula which is applicable to serial correlations, though it contains two coefficients whose estimation itself " presents considerable difficulties ". In the present case there is quite evidently no appreciable trend and it need not therefore be considered, but it remained to determine how far it was necessary to consider the fact that the data are undoubtedly serially correlated. It occurred to me that by taking only every third month in all years combined (*e.g.*, March, June, September and December) I could test whether the strength of the correlation was reduced by thus eliminating the serial correlation effect due to season. Apparently this effect is at any rate not large, for I find for *G. pallidipes* correlation coefficients of −0·86 for months 3, 6, 9 and 12 (as suggested above); −0·90 for months 2, 5, 8 and 11; and −0·88 for months 1, 4, 7 and 10. These coefficients can be compared with −0·90 for the whole series. I therefore think that I am justified in using the ordinary "z" tests, as I have done, to find whether my correlations differ significantly from one another.

Summary.

The mean size of the males of the three tsetse species *Glossina pallidipes*, *G. morsitans* and *G. swynnertoni* is negatively correlated with the mean 2 p.m. saturation deficit of 2 months before.

The correlation is highest (−0·90) for *G. pallidipes*, the largest species, and lowest for *G. swynnertoni*, the smallest. The variation coefficient of mean vein length also is highest for *G. pallidipes* and lowest for *G. swynnertoni*.

The reason for the apparent 2 months' lag in the effect of saturation deficit on size of flies is that the mean male pupal period is 35 days in Shinyanga (23°C.) and the mean age of males measured is 3–4 weeks. If 1 month's lag is tried, the correlation for *G. pallidipes* drops from −0·90 to −0·32, and with no lag at all it is −0·24. The correlation with maximum temperature of 2 months earlier is insignificantly lower than that with saturation deficit; it is −0·79 for *G. pallidipes*.

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THE SANDFLIES (PHLEBOTOMINAE) OF IRAQ.

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The sandflies of Iraq have already received some attention from taxonomists. Newstead (1920) described specimens collected in south Iraq during the first World War. Adler and Theodor (1929) carried out an intensive survey of this subfamily in Iraq, with particular reference to the epidemiology of oriental sore ; their work was, however, limited to a study of the fauna in the urban areas of Baghdad, Mosul and Basrah.

The author, utilising facilities created for the study of the country's Anopheline fauna, carried out a wider survey of the sandfly fauna than had hitherto been practicable. This work was begun in the autumn of 1949 and continued, when the occasion permitted, throughout 1950. The identification of the specimens collected was made possible through the generous assistance of U.N.E.S.C.O., who arranged for the provision of photostat copies of all the rarer references required.

The system of classification adopted is that suggested by Theodor (1948), whose valuable paper provided all the necessary basic data. The author is also indebted to Professor Theodor for advice on the examination of material.

Brief notes on the 12 species taken in the survey are given. Of these one is described as new and two represent new varieties. The distribution of the species within Iraq, with a table showing the distribution of these and other species in neighbouring territories, is also given, and in addition keys for the identification of those species dealt with.

Phlebotomus.

SUBGENUS *Phlebotomus.*

1. **Phlebotomus papatasi** (Scop.).

Bibio papatasi Scopoli 1786, Delic. Faun. Flor. Insubr., **1,** p. 55.

This was the first species to be captured in 1950, when two females were taken on 1st April. With a view to obtaining a correlation between soil temperatures and emergence, a number of observations of the former were made in the author's garden in Baghdad during March and April 1950. It was noted, in shaded ground, that the maximum temperature at a depth of about 10 cm. lay between the mean atmospheric temperature of the previous day and that of the day of observation. At this depth, the soil warmed to 60°F. about mid-March, reached 63°F. on 21st March, and 65°F. for the first time in the afternoon of the 25th March. Thereafter the soil temperature fell to nearly 60°F. and did not reach 65°F. again until the 2nd April—after the first adults had been observed. It would seem therefore that at least some larvae had over-wintered in the superficial layers of the soil, where they would be exposed to higher diurnal maxima than those noted at a depth of 10 cm. After the 2nd April the soil temperatures rose steadily, reaching 70°F., at the same depth, by the 6th April. The first attack by this species was noted by the author on the evening of the 15th April, by which time a few adult *P. papatasi* were in general evidence. The species almost entirely disappeared, however, from the third week in April until mid-May, when it increased rapidly. The small number of this, and other, species noted during April and May implies that the mortality among overwintering forms is heavy and it can be presumed that those which appeared in late May and early June were of the first 1950 generation.

The species was rare by the end of October 1950. It would appear then that the suspension of development in the larva takes place with higher mean atmospheric temperatures than are required for its re-activation.

Nearly 50 per cent. of the females of this species, taken in Baghdad, showed evidence of having taken a recent blood-meal. Only 2 per cent. however had obviously developed eggs in the ovaries, a surprisingly low figure if, as Young and others (1926) claim, this species spends the interval between feeding and oviposition indoors. The author suggests that a large proportion of gravid females pass the period just prior to oviposition in some other resting place—possibly, and most reasonably, in the immediate vicinity of a suitable oviposition site.

The appearance for the first time of this species in large numbers in June is interesting, as this is the month usually associated with outbreaks of sandfly fever in Iraq.

Only one female, recently fed, was noted to be harbouring a mite ectoparasite. It was taken in Baghdad in August.

SUBGENUS *Paraphlebotomus.*

2. **Phlebotomus sergenti** Parrot.

Parrot 1917, Bull. Soc. Path. exot., **10,** p. 564.

No particular search was made for this species, and this factor may explain why it did not figure as prominently in our collections from Baghdad City as it did in those of Adler and Theodor (1929).

The association of this species with human dermal leishmaniasis was close throughout the country, but not absolute. A single specimen from Batas, in Erbil Liwa, and from Suq-us-Shuyukh, in Muntafik Liwa, were from areas free from human infection with *Leishmania tropica.* One-third of the females had evidently taken a recent blood-meal and 7 per cent. had obvious egg-development.

The Iraqi specimens would appear to resemble those from Sind rather than Mediterranean forms—in no instance does the ascoid reach the end of the antennal segment.

3. **Phlebotomus alexandri** Sinton.

P. sergenti var. *alexandri* Sinton 1928, Indian J. med. Res., **16,** p. 308.
P. alexandri Parrot 1938, Arch. Inst. Pasteur Algérie, **14,** p. 428.

This species was recorded as common in Amara by Newstead (1920) and was also noted by the same author from Baquba, Dyala Liwa. It was not however recorded from Iraq by Adler and Theodor (1929).

Its capacity as a vector of dermal leishmaniasis has not been investigated but its rôle in nature, in the areas visited during this survey, would be limited by its comparative rarity. It is unfortunate that no collecting was carried out in Amara town, not only to confirm that this species was still plentiful there, but to throw light on the curious fact that whereas human dermal leishmaniasis is very rare in this town, canine cases are common and cases of canine visceral leishmaniasis have been reported also from this area. This dissociation between human and animal cases of dermal leishmaniasis may also exist in other towns, *e.g.*, Kirkuk, and is a matter which demands further investigation. A rapid and simple method of separating this species from *P. sergenti* may therefore be of importance in epidemiological studies of the mammalian leishmanias of this region. The identification of specimens which have undergone dissection in saline is not easy, and for this reason a note on the separation of this species from *P. sergenti*, from the length of the third antennal segment, has been included (see Table I).

TABLE I.

Measured length of the third antennal segment in 25 female and 25 male *P. sergenti* and in 14 female and 21 male *P. alexandri* adult sandflies.

	Mean.	Range	σ
P. sergenti ♀	0·24 mm.	0·210–0·270 mm.	0·014 mm.
„ ♂	0·250 mm.	0·218–0·290 mm.	0·020 mm.
P. alexandri ♀	0·141 mm.	0·105–0·165 mm.	0·018 mm.
„ ♂	0·144 mm.	0·113–0·175 mm.	0·011 mm.

None of the female *P. alexandri* examined had taken a recent blood-meal ; this was doubtless due to the fact that most of the specimens were caught in the evening round a light in the author's garden. No example was seen with obvious egg-development.

SUBGENUS *Larroussius*.

4. **Phlebotomus wenyoni** Adler & Theodor.

Adler & Theodor 1930, Bull. ent. Res., **21**, p. 535.

Seven females were taken at Salahuddin, which is 3,500 ft. above sea level, in September. One had taken a recent blood-meal.

This important subgenus is poorly represented in Iraq but it is possible that a more intensive search than that conducted by the author would reveal the presence of other species, particularly in the north-west of the country. At least one case of human visceral leishmaniasis has been suspected from the Zakho area of Mosul Liwa and further studies of the sandfly fauna of this locality are indicated.

Sergentomyia.

SUBGENUS *Sergentomyia*.

Group *minuta*.

5. **Sergentomyia hodgsoni** (Sinton).

Phlebotomus hodgsoni Sinton 1933, Indian J. med. Res., **20**, p. 874.

One female and one male of this species was collected at Salahuddin in August and a further female in September.

This species was placed by Theodor (1948) in the subgenus *Sintonius*, presumably on account of the segmentation of the spermatheca described and sketched by Sinton (1933b). The author's view is that the marking on the spermatheca was not true segmentation and was invisible, even in the dissected organ, until clearing was complete ; it then appeared as a tracery of fine, transverse reticulations. This species in all other respects resembles *S. minuta* var. *parroti* Adler & Theodor, and it has accordingly been moved into the " Group *minuta*."

Group *fallax*.

6. **Sergentomyia theodori babylonica,** var. n.

This species was widely distributed in central and southern Iraq. Among the females examined only one showed evidence of having taken a recent blood-meal and about 8 per cent. had well-developed eggs in the ovaries.

Female.

Mean length (anterior border of thorax to tip of abdomen) : 1·6 mm. (range 1·4 mm.–1·9 mm.).

Mean length of thorax : 0·43 mm. (0·40–0·46 mm.).

Antennal segment III.—Mean length : 0·081 mm. (0·072–0·088 mm. ; σ among 50 specimens was 0·004 mm.). Ascoids usually just over one-quarter of the length of the segment.

Epipharynx.—0·09–0·12 mm. $\frac{A}{E}$: 0·74–0·92.

Palpi.—Formula : 1, 2, 3, 4, 5, rarely 1, 2 (3, 4), 5.

Wing.—Mean length : 1·3 mm. (1·1–1·4 mm.). Mean breadth : 0·28 mm. (0·26–0·29 mm.). L/Br. : about 4·8. α/β : 0·35–0·7.

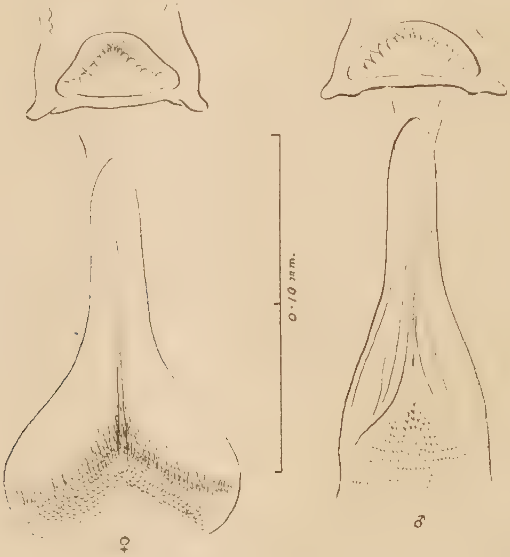


Fig. 1.—Buccal cavity and pharynx of *S. theodori* var. *babylonica.*

Buccal cavity (fig. 1).—Sixteen to twenty pointed teeth on a deep arc with the convexity anteriorly. The four or five medial teeth are usually reduced in size and are set relatively closely together. The pigmented area is normally faint, and when present, is a diffuse oval superimposed on the central teeth in the armature.

Pharynx (fig. 1).—Proportion of length to breadth varies from 1·5 to 2. The armature consists of spines which originate in rows roughly parallel to the deeply indented posterior margin. The anterior spines are stout, the posterior ones short and refractile.

Spermatheca.—See fig. 10.

Male.

Mean length : 1·6 mm. (1·4–1·78 mm.).

Mean length of thorax : 0·41 mm. (0·35–0·45 mm.).

Antennal segment III.—Mean length : 0·110 mm. (0·1–0·115 mm.). Ascoids about one-sixth of the length of the segment.

Epipharynx.—0·11–0·13 mm. $\frac{A}{E}$: 0·89–1·03.

Palpi.—Formula : usually 1, 2, 3, 4, 5, rarely 1, 2 (3, 4), 5.

Wing.—Mean length : 1·32 mm. (1·25–1·37 mm.). Mean breadth : 0·24 mm. (0·2–0·26 mm.). L/Br. : about 5·5. α/β : 0·38–0·61.

Buccal cavity (fig. 1).—Armature consists of 14–18 pointed teeth on an arc with the convexity anteriorly. Gradation between the lateral and medial teeth not marked and may be difficult to demonstrate. Pigmented area usually absent ; when present, like that of the female.

Pharynx (fig. 1).—2·5–3 times as long as broad. The armature consists of a series of weak, more-or-less transverse ridges, each bearing a row of minute, refractile teeth. There are also a few weak, scattered spines in the antero-medial portion of the armature.

Genitalia.—Coxite has a mean length of 0·27 mm. (0·26–0·3 mm.), and is about four times as long as broad. The style (fig. 2) has a mean length of 0·115 mm. (0·085–0·13 mm.). The longest spine is usually a little shorter than the style. All the spines arise terminally. The seta is weakly developed and arises about one-fifth from the distal extremity of the style. The penis (fig. 2) is about 0·095 mm. in length and is similar in shape to that of *S. theodori* (Parrot). The paramere (fig. 2) is clubbed and is about 0·04 mm. shorter than the inferior clasper.

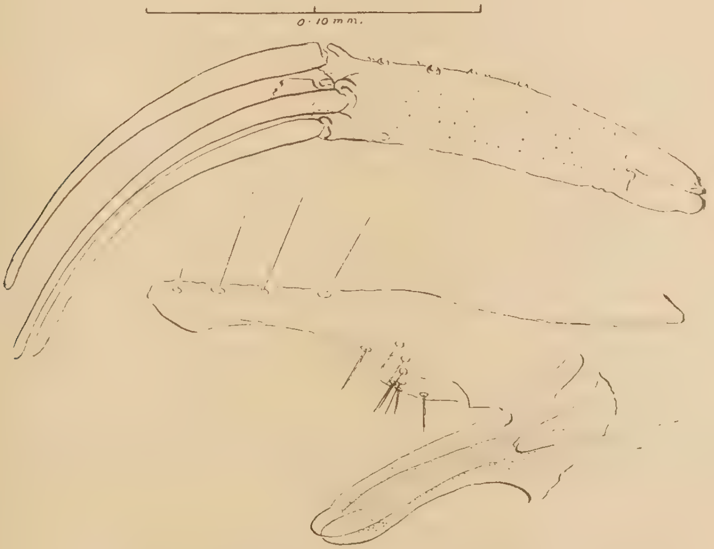


Fig. 2.—Style, paramere and penis of *S. theodori* var. *babylonica.*

This sandfly, though closely related to *S. theodori*, has been given varietal status for the following reasons. There are fewer teeth in the buccal armature, and these show less differentiation into large lateral and small medial, than in the type species. The pigmented area is also less conspicuous and of a different shape. The pharynx is relatively broader than that of the type. A further point of some importance, is that this variety appears to be strictly confined in Iraq to the Saharo-Sindian zoogeographical region. As it does not enter the Irano-Turanian region here, it is unlikely to appear in Syria and northern Israel, where the type is widespread. It is believed that this is an eremic form of the type, which, in this and other respects, is a form intermediate between *S. theodori* and *S. punjabensis* (Sinton) (1933b).

This is the form recorded from Iraq as *minutus* Rondani by Adler and Theodor (1929), and from Amara as *P. antennatus* var. by Newstead (1920), which had the short antennal segment III, once considered characteristic of *P. antennatus* (Newst., 1912).

Professor Theodor (recent personal communication) had apparently already recognised that the Iraqi specimens of *S. theodori* belong to a separate race. He also notes that the typical form is replaced by this form in the neighbourhood of the Dead Sea. As the Dead Sea area represents a northerly extension of the Saharo-Sindian zoogeographical region, the occurrence of var. *babylonica* is some confirmation of the opinion expressed above that this form is strictly eremic in distribution.

Types and paratypes have been lodged provisionally in the Directorate of Endemic Diseases, Baghdad.

7. **Sergentomyia sintoni,** sp. n.

This species was encountered in small numbers on the outskirts of Baghdad city and in a few other localities in central Iraq.

Female.

Mean length : 1·8 mm. (1·75–1·9 mm.).

Mean length of thorax : 0·49 mm. (0·47–0·53 mm.).

Antennal segment III.—Mean length : 0·103 mm. (0·095–0·114 mm., σ: 0·005 mm.). Ascoids about one-quarter of the length of the segment.

Epipharynx.—0·14–0·154 mm. $\frac{A}{E}$: 0·62–0·72.

Palpi.—Formula : 1, 2, 4, 3, 5, or 1, 2 (3, 4), 5. Relative length of segments 1 : 2 : 3·6 : 3·2 : 6·6.

Wing.—Mean length : 1·5 mm. (1·25–1·6 mm.). L/Br. : about 5·3 (4·8–5·6). α/β : 0·3–0·7.

Buccal cavity (fig. 3).—Armature consists of 12–14 easily definable teeth on a moderate arc with the convexity anteriorly. The teeth are evenly spaced throughout, though the medial teeth may be somewhat shorter than the lateral teeth. There is usually a dark pigmented area present, of a roughly triangular shape with rounded corners.

Pharynx (fig. 3).—About twice as long as broad. The armature consists of a group of dark, elongated, blunt spines.

Spermatheca (fig. 11).—This organ resembles that of *S. theodori* var. *babylonica* but is relatively short in proportion to its breadth.

Male.

Mean length : 1·68 mm. (1·6–1·8 mm.).

Mean length of thorax : 0·42 mm. (0·39–0·45 mm.).

Antennal segment III.—Mean length : 0·146 mm. (0·142–0·152 mm.). Ascoid one-seventh to one-ninth of the length of the segment.

Epipharynx.— 0·12–0·133 mm. $\frac{A}{E}$: 1·07–1·21.

Palpi.—Formula usually 1, 2 (3, 4), 5. Relative length of segments : 1 : 2 : 3·7 : 3·7 : 7·3.

Wing.—Mean length : 1·32 mm. (1·3–1·36 mm.). Mean breadth : 0·25 mm. (0·24–0·27 mm.). L/Br. : 5–5·6. α/β : 0·35–0·7.

Buccal cavity (fig. 3).—Armature consists of 10–14 pointed teeth, evenly spaced and often very indistinct ; situated on a shallow arc with the convexity anteriorly. There is usually a small, irregular pigmented area.

Pharynx (fig. 3).—Three to four times as long as broad. The armature consists of a number of weak, transverse ridges, each crowned by a row of minute teeth. There may also be a few long, weak spines arising in the mid-line just anterior to this armature.

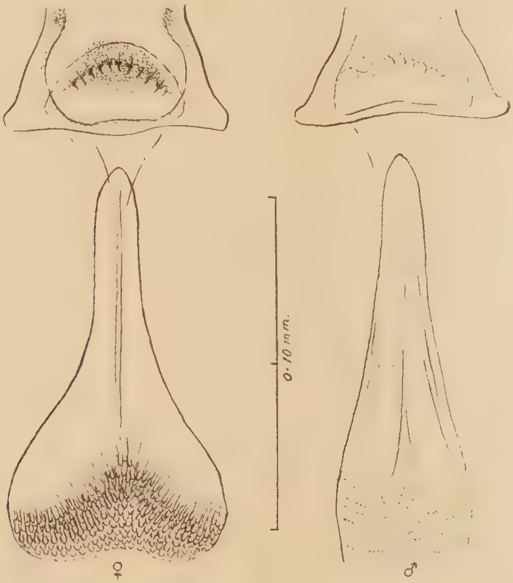


Fig. 3.—Buccal cavity and pharynx of *S. sintoni.*

Genitalia.—Coxite averages 0·225 mm. in length (0·206–0·23 mm.), and is four to five times as long as broad ; it is always about two and a half times the length of the style which has a mean length of 0·09 mm. (0·088 0·097 mm.). The spines (fig. 4), at least one of which is appreciably longer than the style, arise from two terminal, and two sub-terminal roots. The seta is well developed, being about 0·03 mm. in length, and originates on a level with the roots of the sub-terminal spines—about one-fifth from the distal extremity of the style. The penis (fig. 4) is slender with a dorsal, sub-terminal notch. The paramere (fig. 4) tapers to a finger-like termination, only rarely is there any suggestion of clubbing. It is overlapped by the inferior clasper by about 0·02 mm.

In the arrangement of the buccal teeth in the female, this species resembles the form regarded by Sinton (1932) as " *P. minutus*, Rondani ", from Pakistan. It also resembles that of *S. fallax* var. *cypriotica* (Adler) from which it differs in the shape and armature of the pharynx. The male also resembles that described as " *P. minutus*, Rondani " by Sinton (1933~~b~~), and it is considered that the Iraqi material belongs to the same species as that wrongly named by Sinton as *minutus* Rondani. It is therefore necessary to give it a name, and, in recognition of the important studies on the /c taxonomy of sandflies carried out by Brigadier Sinton, the species has been named after that worker.

Types and paratypes have been lodged provisionally in the Directorate of Endemic Diseases, Baghdad.

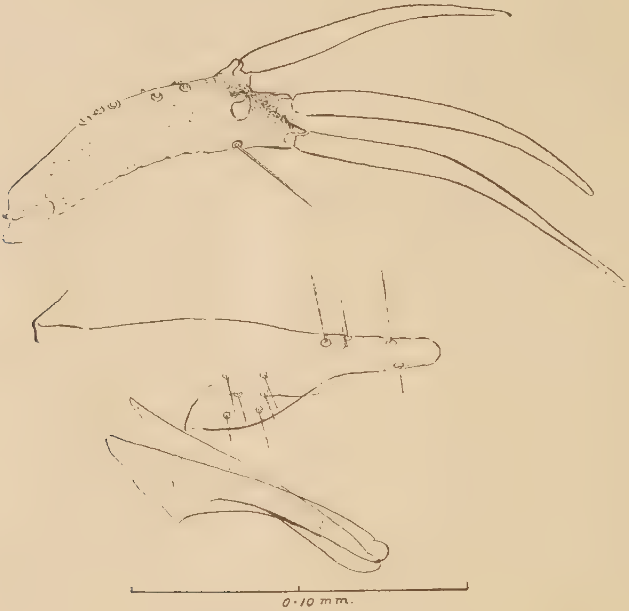


Fig. 4.—Style, paramere and penis of *S. sintoni.*

8. **Sergentomyia dentata mediensis,** var. n.

This species was found in three localities in Iraqi Kurdistan above 2,000 ft. above sea level, and was common at Salahuddin (3,500 ft.). It was taken there between June and September. Neither fed nor gravid females were noted.

Female.

Mean size : 1·87 mm. (1·6–2·0 mm.).

Mean thoracic length : 0·5 mm. (0·48–0·56 mm.).

Antennal segment.—Mean length : 0·116 mm. (0·095–0·137 mm., σ: 0·009 mm.). Ascoids about one-fifth of the length of the segment.

Epipharynx.—0·15–0·172 mm. $\frac{A}{E}$: 0·66–0·78.

Palpi.—Rather variable, segment 3 may be equal to, longer or shorter than, segment 4. Relative length of segments : 1 : 2·3 : 4 : 4·1 : 8.

Wing.—Mean length : 1·5 mm. (1·31—1·65 mm.). Mean breadth : 0·3 mm. (0·24–0·34 mm.). L/Br. : about 5. α/β : about 0·39 (0·24–0·6).

Buccal cavity (fig. 5).—Armature consists of about 20 sharply pointed teeth on a deep arc with the convexity anteriorly. The medial six or eight teeth are greatly reduced in size and laterally compressed. There is a very constant dark pigmented area, shaped like the segment of an orange, with the outer curve following roughly the edge of the buccal plate.

Pharynx (fig. 5).—Usually about 2·3 times as long as broad, but this proportion varies from 2·1 to 2·9. The armature consists of a mass of deeply pigmented, strong, blunt spines. The anterior rows are elongated. The posterior margin of the pharynx is nearly straight.

Spermatheca (fig. 11).—The terminal umbilication is more marked in this species than in any other of this group from Iraq. The duct is only slightly narrower than the broadest part of the organ.

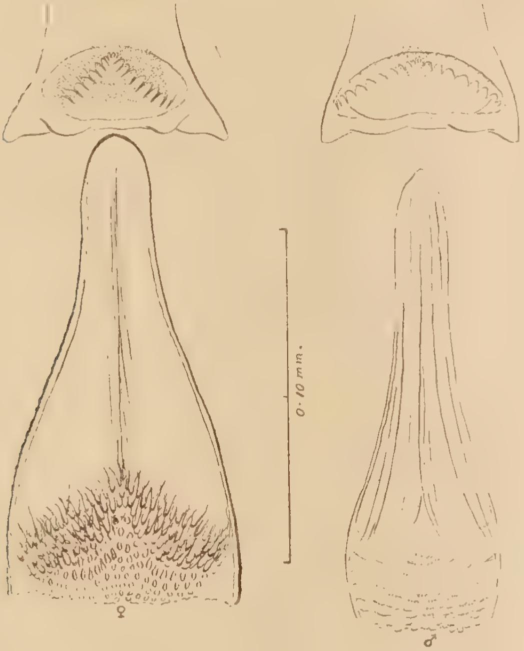


Fig. 5.—Buccal cavity and pharynx of *S. dentata* var. *mediensis.*

Male.

Mean length : 1·8 mm. (1·6–2·0 mm.).

Mean length of thorax : 0·45 mm. (0·44–0·48 mm.).

Antennal segment III.—Mean length : 0·145 mm. (0·13–0·168 mm.). Ascoids from one-ninth to one-twelfth of the length of the segment.

Epipharynx.—0·13–0·153 mm. $\frac{A}{E}$: 0·87–1·1.

Palpi.—Usual formula : 1, 2 (3, 4), 5 ; may also be 1, 2, 4, 3, 5. Relative lengths of segments : 1 : 2·5 : 4 : 4 : 7·7.

Wing.—Mean length : 1·45 mm. (1·38–1·53 mm.). Mean breadth : 0·25 mm. (0·22–0·27 mm.). L/Br. : about 5·7. α/β : about 0·3 (0·17–0·49).

Buccal cavity (fig. 5).—About 20 clearly definable teeth in the armature. About 15 are moderately developed and the four medial teeth are small. The pigmented area is smaller and paler than that of the female, and may be hardly distinguishable.

Pharynx (fig. 5).—More than three times as long as broad. The armature resembles that of *S. sintoni*, but is less extensive.

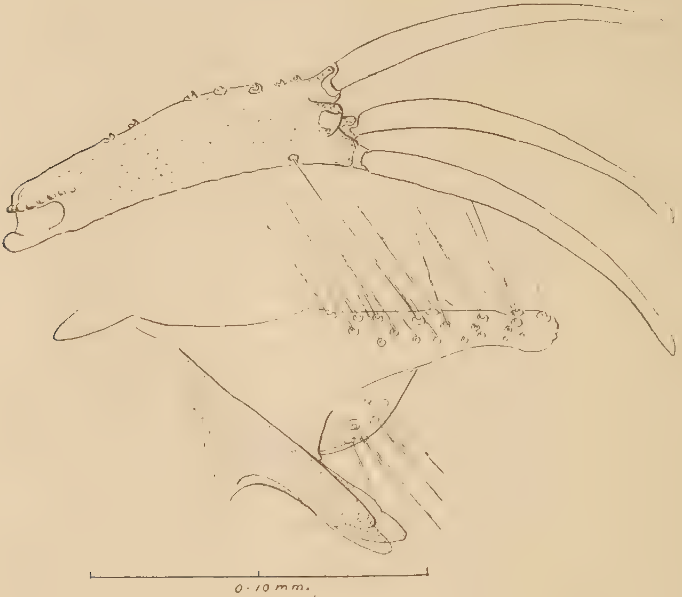


Fig. 6.—Style, paramere and penis of *S. dentata* var. *mediensis*.

Genitalia.—The mean coxite length is 0·26 mm. (0·25–0·27 mm.). The style (fig. 6) measures about 0·113 mm. (0·108–0·12 mm.). The longest spine is about the same length as the style. Two of the spines arise somewhat sub-terminally. The seta is weakly developed and arises between one-quarter and one-fifth from the distal extremity of the style. The penis (fig. 6) resembles that of *S. theodori* and measures from 0·09 to 0·10 mm. The paramere (fig. 6) is slightly clubbed but is more slender than in *S. theodori*, and is overlapped by the inferior clasper by about 0·025 mm.

This species is darker in colour than other species of the group from this area. The buccal armature in the female is intermediate in appearance between *S. dentata* (Sinton, 1933a) and *S. theodori* (Parrot) but it bears a strong resemblance to the former species in the pharyngeal armature, the spermatheca and the male genitalia. As there is such a degree of divergence in the appearance of the buccal cavity in the females, this species has been placed provisionally as a variety of *S. dentata*. The name "*mediensis*" was selected as the ancient kingdom of the Medes was centred in the mountainous region from which these specimens were obtained.

Types and paratypes have been lodged provisionally in the Directorate of Endemic Diseases, Baghdad.

9. **Sergentomyia mervynae,** sp. n.

Two females and one male were taken in Kerbela City in October 1950.

Female.

Mean length : 2·1 mm. (paratype : 2·2 mm.).

Length of thorax : 0·52 mm.

Antennal segment III.—Length : 0·98 mm. (paratype : 0·114 mm.). Ascoids about 0·025 mm. in length and about one-quarter the length of the segment.

Epipharynx.—0·153 mm. (paratype : 0·166 mm.). $\frac{A}{E}$: 0·64 (paratype : 0·66).

Palpi.—Formula : 1, 2, 3, 4, 5. Relative length of segments : 1 : 2 : 3·7 : 4 : 7·5 (paratype : 1 : 2·5 : 4 : 4·4 : 9·3).

Wing.—Length : 1·47 mm. (paratype : 1·57 mm.). L/Br. : 4·4. α/β :0·47.

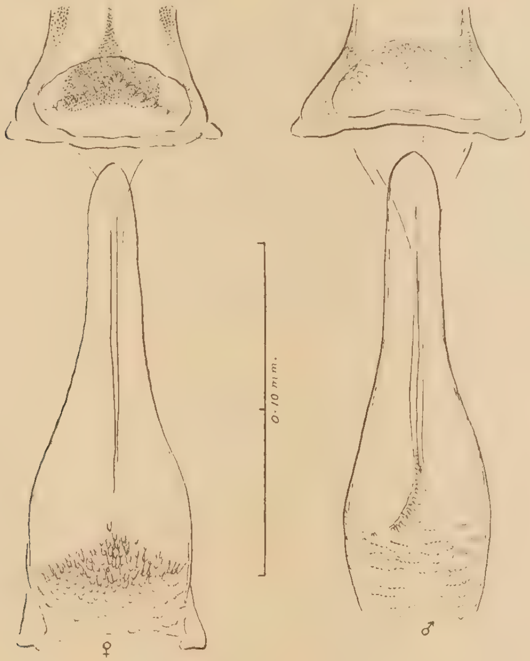


Fig. 7.—Buccal cavity and pharynx of *S. mervynae.*

Buccal cavity (fig. 7).—The armature consists of about 16 long, rather indistinct teeth, whose serrations are abnormally separated from the edge of the buccal plate. They are somewhat obscured by a large, densely pigmented area, which has, in both females, a clearly marked tapering extension which is produced forwards in the mid-line.

Pharynx (fig. 7).—About three times as long as broad. The armature consists of a group of long, brown spines bunched centrally so that their posterior margin presents a strong curve with the convexity posteriorly. The remainder of the pharynx posterior to these spines is scarcely armed.

Spermatheca (fig. 10).—This organ differs markedly from all other species in this group from Iraq. The terminal umbilication is almost absent in both examples and the duct is narrower than in the other species examined.

Male.

A single male, taken at the same time, and in the same place, as the two females, will be described as the apparent male of this species.

Length : 1·86 mm. Length of thorax : 0·43 mm.

Antennal segment III.—0·142 mm. Ascoids 0·015 mm. in length and so about one-ninth of the length of the segment.

Epipharynx.—0·15 mm. $\frac{A}{E}$: 0·98.

Palpi.—Formula : 1, 2 (3, 4), 5. Relative length of segments : 1 : 3 : 5 : 5 : 11.

Wing.—1·46 × 0·27 mm. L/Br. : 5·4. α/β : 2·9 and 2·2 (variation between the two wings).

Buccal cavity (fig. 7).—About 20 weakly chitinised, blunt teeth. There is an irregularly shaped, greyish-brown, pigmented area in the centre of the armature.

Pharynx (fig. 7).—Length just over three times the maximum breadth. The armature resembles that of the male of *S. sintoni* but is less extensive.

Genitalia.—The coxite measures 0·26 × 0·059 mm. It is 2·28 times as long as the style, which measures 0·114 mm. (fig. 8). The longest spine which is slightly shorter than the style, arises from a prominent tubercle which is produced distally beyond the other tubercles. The seta measures 0·02 mm. in length and arises about one-fifth from the distal extremity of the style. The penis (fig. 8) resembles that of *S. theodori* and is 0·093 mm. in length. The paramere (fig. 8) is 0·153 mm. in length and is 0·025 mm. shorter than the inferior clasper.

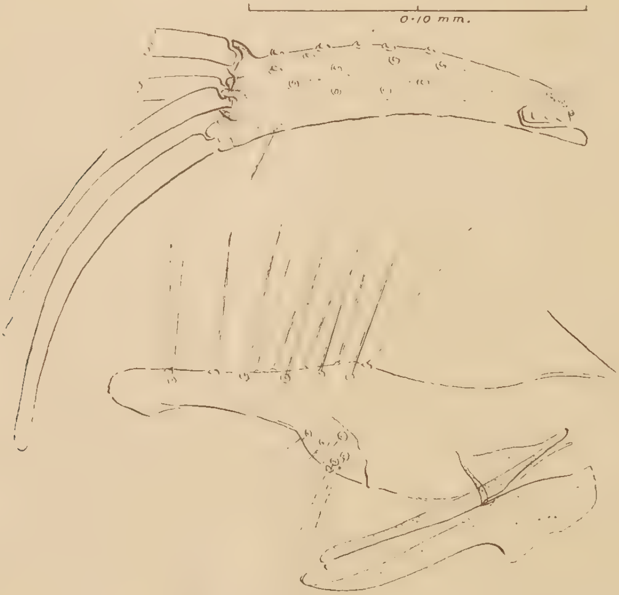


Fig. 8.—Style, paramere and penis of *S. mervynae.*

The female of this species can be separated from nearly all other allied types by the curious pattern of teeth in the pharyngeal armature. The only species known to the author which it resembles in this respect is *S. yusafi* (Sinton 1930), the status of which is also discussed by Theodor (1931) and Kirk and Lewis (1946). (The illustration in the keys produced by the last authors, of the female pharynx of *S. yusafi*, is rather inconsistent with the illustrations of the same structure produced by the two earlier authorities.) In other respects, however, this species is clearly different from *S. yusafi* and it has been dedicated to my wife, whose generous support and interest in the survey greatly lightened the task.

The types and paratype have been lodged provisionally in the Directorate of Endemic Diseases, Baghdad.

10. **Sergentomyia baghdadis** (Adler & Theodor).

Adler & Theodor 1929, Ann. trop. Med. Paras., **23,** p. 281.

This species appears to have a wide distribution over the southern part of Iraq and is often common. As with *S. theodori* var. *babylonica*, this species does not encroach into the Irano-Turanian steppe desert of the north of Iraq. It was taken from 7th June until 20th November (Basrah). Among 131 females, 20 per cent. had taken a recent blood-meal and 18 per cent. had well-developed eggs. Gravid females with traces of fresh blood in the stomach were also noted not infrequently in this species.

11. **Sergentomyia palestinensis** (Adler & Theodor).

Adler & Theodor 1927, Ann. trop. Med. Paras., **21,** p. 64 (♀) ; Theodor, 1947, Bull. ent. Res., **38,** p. 96 (♂).

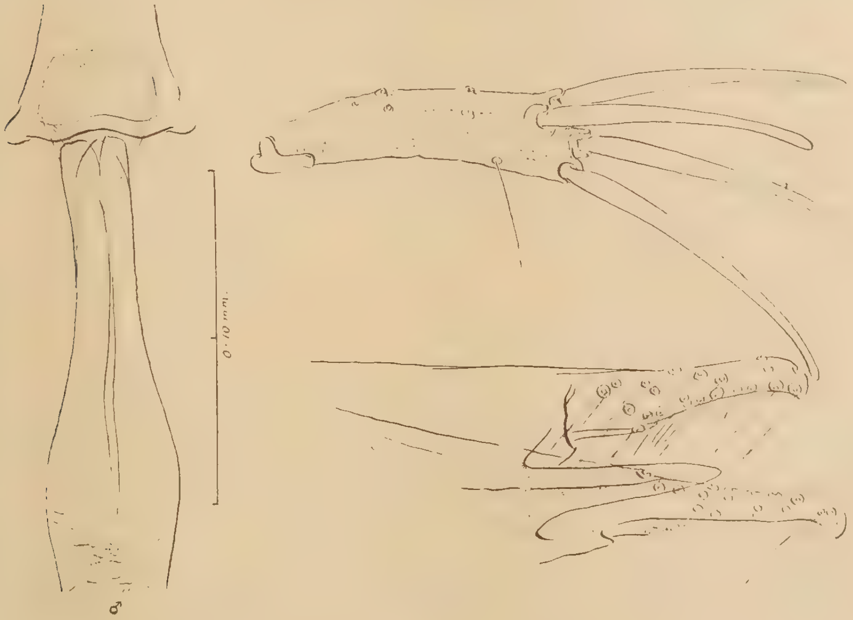


Fig. 9.—Buccal cavity, pharynx, style, paramere and penis of *S. palestinensis*.

This species appears to be rare in Iraq. Adler and Theodor recorded only three females from Iraq, while the author took 15 females and one male in this survey. Most of the specimens were obtained round an outdoor light in the author's garden in Baghdad, one female was taken in another garden in Baghdad, on an April morning, resting on a wall in the shade. This species may therefore be more obligatory sylvan than other, more conspicuous, species.

The male of this species was described by Theodor from a single example caught in Jericho in July, 1934. The male referred to in this survey was taken in a day catch from Karradat Sheriqiyeh, Baghdad city, in June. As this specimen differs in some details from that described by Theodor, it has been considered justifiable to include here a description of the Baghdad specimen.

Unfortunately only the head and genitalia were mounted.

Antennal segment III.—(The antennae were missing from the type specimen.) Length : 0·184 mm. Ascoids extraordinarily short (as they are in the female), being about 0·008 mm. in length and so less than one-twentieth of the length of the segment.

Epipharynx :—0·12 mm. $\frac{A}{E}$: 1·37.

Palpi.—Relative length of segments : 1 : 2·8 : 3·7 : 4 : 8.

Buccal cavity (fig. 9).—Differs from that figured by Theodor in that there are six distinct, but weakly chitinised, teeth with a number of indistinct shorter spines interspersed between them. The teeth arise in almost a straight line. There is no trace of a pigmented area.

Pharynx (fig. 9).—Probably similar to that figured by Theodor, though examination of the armature with an oil-immersion lens revealed that the ridges in the pharynx are surmounted by a row of minute teeth. The size of the pharynx in this specimen is 0·14 × 0·04 mm.

Genitalia.—The coxite is 0·22 × 0·65 mm. The style (fig. 9) measures 0·096 mm. in length. The longest spine is slightly longer than the style. The spines arise with one pair terminally and one pair just sub-terminally, as sketched from the Jericho example. The seta measures 0·035 mm. in length and originates about one-third of the length of the style from the distal extremity. The penis (fig. 9) measures 0·11 mm. in length and exactly resembles that of Theodor's sketch. The paramere is also identical with the type and is about 0·02 mm. shorter than the inferior clasper.

Group *squamipleuris*.

12. **Sergentomyia squamipleuris** (Newstead).

Phlebotomus squamipleuris Newstead 1912, Bull. ent. Res., **3,** p. 366.

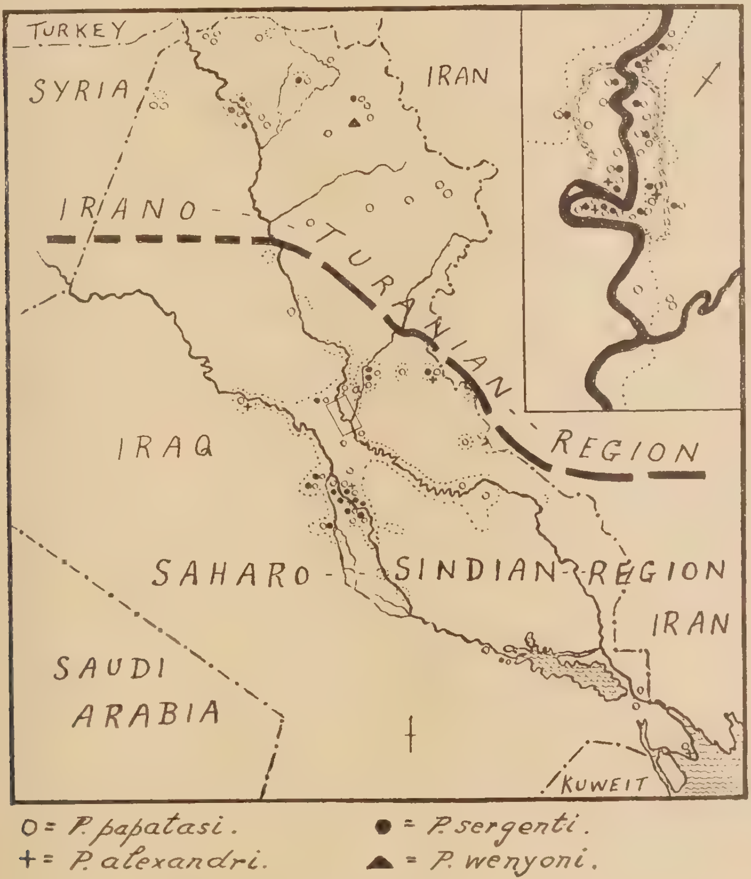
This species would appear to be local in distribution. It came to light in Baghdad in much greater numbers than could be found in the same area by day. It appeared first in Baghdad on the 4th April, only three days later than the first recorded sandfly of the season. It was the last species recorded in 1950, a few being caught near Kerbela on 25th and 26th November.

The Iraqi specimens resemble those from Africa rather than those from India, which were given varietal status by Theodor (1931), but the Iraqi specimens examined by the author have fewer teeth in the buccal armature than the type form from Africa.

Among the Baghdad females about 2·5 per cent. had taken a blood meal just prior to capture and about 13 per cent. had well-developed eggs. The proportion of gravid females fell to below this figure during November.

Distribution in Iraq and neighbouring Territories.

The relationship between the distribution of human dermal leishmaniasis and of species of the genus *Phlebotomus* is indicated in Map 1. The evidence there supports the present belief that *P. sergenti* is the principal, if not the sole, vector of oriental sore in Iraq. Unfortunately the numbers collected were too few to admit of any conclusions to be drawn from the apparent absence of this species in certain endemic foci, for example, Ramadi.


TURKEY
SYRIA
IRAN
IRANO-TURANIAN REGION
IRAQ
SAHARO-SINDIAN REGION
IRAN
SAUDI ARABIA
KUWEIT
O = P. papatasi.
● = P. sergenti.
+ = P. alexandri.
▲ = P. wenyoni.

Map 1.

Map of Iraq (1 : 7,200,000) showing international boundaries and main rivers with, inset, a rough map of the Baghdad City area on a scale of about 1 : 600,000.

Areas with a moderate to high endemicity of dermal leishmaniasis in man are enclosed in dotted lines.

The approximate dividing line between the Saharo-Sindian and Irano-Turanian zoogeographical regions is indicated by the thick, interrupted line. (The course of this boundary in the Syrian desert is not known.)

The distribution of species of the genus *Phlebotomus* is shown.

The reason for the absence of this species from the south of Iraq is a question of great practical importance. Climatic factors can be excluded as a reason for this, as the south does not experience the extremes of heat or cold met with in the centre of the country. The only reasonable supposition is the existence, in the southern area, of soil conditions unsuitable for the species in its larval stage. This supposition gains support from the fact that the species is found in rural areas only where these are irrigated by high-level canals. In contrast with areas not irrigated in this manner, these districts would offer large areas of ground with a high, and very consistent, soil-water table.

This species is also abundant in densely populated urban areas over a much wider geographical range than it occurs as a rural species. Nevertheless the above supposition is not thereby invalidated. Even the largest cities of Iraq are as yet without any efficient means of disposal of domestic waste-water. This water is either allowed to percolate into the soil around the buildings or is run off in open earth drains or, most often, is collected into underground pits, which, as they are unlined, function as storage places for the maintenance of a high subsoil water level. Conditions favourable for the breeding of *P. sergenti* in towns are thus maintained. The cities of Baghdad and Mosul, which have little natural drainage for their soil, are certainly highly endemic foci of human dermal leishmaniasis. It is curious therefore, at first sight, that the similar conditions existing within the town of Basrah should not also be associated with the presence there of either the disease or its sandfly vector.

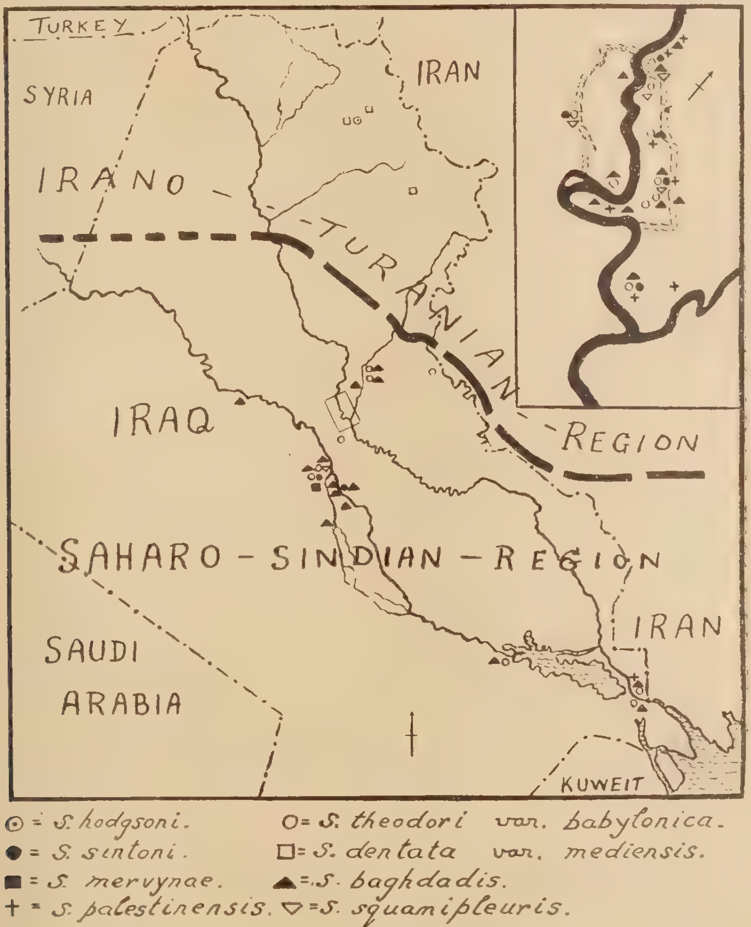
Other large towns which are free from oriental sore in man are Kirkuk and Erbil, but both places have natural drainage slopes and both suffer somewhat from a shortage of water in the town during summer. On the other hand, endemic foci do exist in communities whose houses are apparently well-drained, for example Beled Sinjar, Aqra, Amadia and Mandeli which are all built on sloping ground. Each of these places however has perennial springs, which must create, in their vicinity, conditions suitable for the larvae of *P. sergenti*.

It is suggested that the absence of *P. sergenti* from the town of Basrah, and from many apparently suitable communities in the south of Iraq, is due to the instability of the soil-water table in these areas. Basrah, for instance, lies close to the Shatt-al-Arab river. This waterway, for two months in summer, flows above ground level for a period varying with the intensity of the flood levels in the Tigris and Euphrates rivers. Although the town of Basrah is usually saved from inundation, seepages are widespread and sub-soil water levels rise to near the ground surface. During the remainder of the summer the water-table declines.

If *P. sergenti* is as sensitive to soil-water levels as it appears to be from the above arguments, effective drainage of urban areas in the plains of Iraq might well be followed by the disappearance of this species from such localities and so of dermal leishmaniasis in man. It is to be hoped that this will be put to the test. The important counter-drainage of tracts, irrigated by continuous flow systems, might also be expected to bring about similar benefits. Nevertheless it is also possible that *P. sergenti* utilises the burrows of domestic rodents for breeding and resting, and this may also explain the good adaptation shown by this species to an urban environment.

Further observations on the distribution and epidemiology of oriental sore in Iraq will be presented in a later paper.

The other common species of this genus, *P. papatasi*, has an entirely different distribution in Iraq to *P. sergenti*. As this species is important as the vector of sandfly fever and as a serious summer " nuisance ", it is perhaps desirable to add a few comments to those already made under this species (see p. 707). It occurred from the extreme south to the extreme north and usually predominated in the catch from localities below 3,000 ft. It is abundant, not only in Iraq, but over a remarkable range of environments which have only one important factor in common—a hot season during which rain is rare. A feature which such conditions must inevitably produce, wherever the soil is suitable, is the " earth-crack ". As the heat and drought continues such a crack will extend deeper into the ground, maintaining near its base an equable air temperature and a standardised degree of soil moisture. The light alluvial soil of Iraq is well suited to the development of deep cracks, more friable or shallow soil overlying a dense substratum would be less liable to fissure cleanly to the requisite depth. It is believed that these cracks provide not only a nidus for the larvae of *P. papatasi*, but also ideal resting places for the adults, and it is probable that gravid females spend much of their time before oviposition in this environment. The only area where *P. papatasi* is relatively uncommon at low elevations in Iraq is near to the Shatt-al-Arab. Here, among the date-groves, the soil is never more than superficially dry, and thus the formation of deep cracks, which this species seems to require for breeding, is unlikely.


TURKEY
IRAN
SYRIA
IRANO-TURANIAN-REGION
IRAQ
SAHARO-SINDIAN-REGION
IRAN
SAUDI ARABIA
KUWEIT
⊙ = S. hodgsoni.
● = S. sintoni.
■ = S. mervynae.
+ = S. palestinensis.
○ = S. theodori var. babylonica.
□ = S. dentata var. mediensis.
▲ = S. baghdadis.
▽ = S. squamipleuris.

Map 2.

Map of Iraq (1 : 7,200,000) showing international boundaries and the course of the main rivers with, inset, a rough map of the Baghdad city area on a scale of about 1 : 600,000.

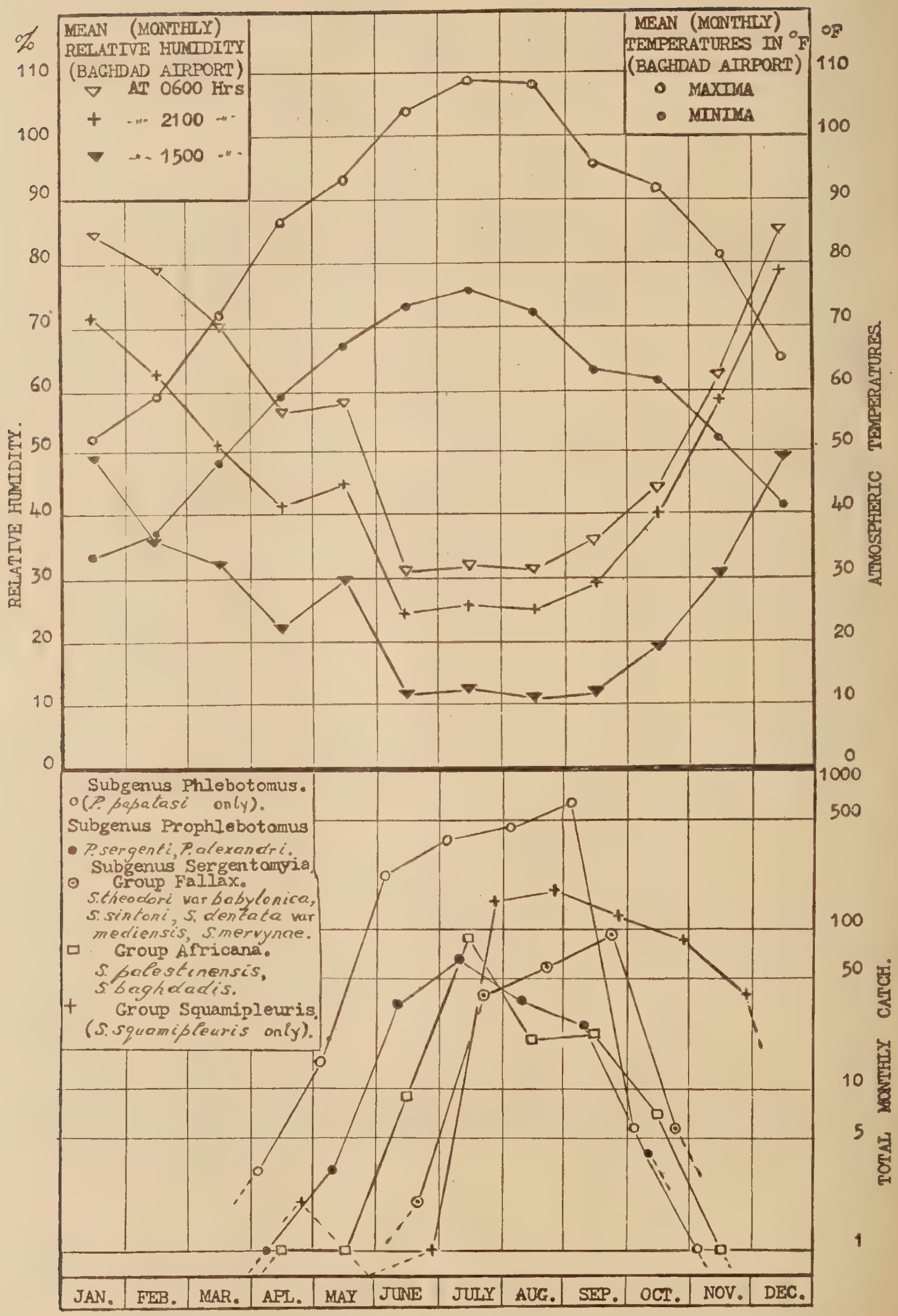
The approximate dividing line between the Saharo-Sindian and the Irano-Turanian zoogeographical regions is indicated by a broad, interrupted line. (The course of this boundary in the Syrian desert is unknown.)

The distribution of sandflies of the genus *Sergentomyia* is shown.

TABLE II. Distribution of Sandflies within Iraq.

Liwa	Locality	Ht. in feet a.s.l.	*P. papatasi*		*P. sergenti*		*P. alexandri*		*P. wenyoni*		*S. hodgsoni*		*S. theodori* v. *babylonica*		*S. sintoni*		*S. dentata* var. *mediensis*		*S. mertynae*		*S. palestinensis*		*S. baghdadis*		*S. squamipleuris*	
			♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Baghdad	Abu Ghuraib ...	120	1	3		2																				
	Baghdad City	100	943	789	70	60	23	18					104	71	15	29					13	1	106	58	505	82
	Fahameh ...	100	5	5	5	7																	15			
	Mahmudiyeh ...	110	25	10									1													
	Rustamiyeh ...	100	175	140																	1					
	Sammarah Stn.	300	10																							
	Suleikh ...	100	17	21		1		2					4	7		1									4	
	Washash ...	100	59	40	1								1		1										1	
	Zaffaraniyeh ...	100	27	21										1		1							4	1		
Basrah	Basrah City ...	10	1	5									1	19									5	3		
	Fao	10	27	1			1																			
	Tanuma ...	10	7	5									1	3							1		4	1		
	Ramadi ...	150	4	16				1																		
Dulaim Dyala	Beled Ruz ...	150	5																							
	Huweidar ...	150	29	20	8								1										1			
	Khan Beni Sa'ad	150	18	15																			2			
	Kharnabat ...	150	8	8	12	14							6										3			
	Mandeli ...	200	14	8		1	1						1													
Erbil	Batas	2,500	6	4	2																					
	Erbil Town ...	1,250	15	2																						
	Salahuddin ...	3,500							7		2	1					68	41								
	Shaqlawa ...	2,300	6	12													1									
	Harir	2,500	5	1																						
	Zibar	1,750	6																							
Kerbela	Daraweesh ...	100	5	18									2										3		15	1
	Kerbela City ...	90	57	32	4								4	2	1				2	1			5	2		
	Kufa Town ...	90	14	9	1																					

Liwa	Locality	Ht. in feet a.s.l.	P. papatasi		P. sergenti		P. alexandri		P. wenyoni		S. hodgsoni		S. theodori v. babylonica		S. sintoni		S. dentata var. mediensis		S. mervynae		S. palestinensis		S. baghdadis		S. squamipleuris	
			♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Hilla	Albu Sabar ...	100	5	4		1																				
	Dabla	100	6	2	3	1																				
	Efariyeh ...	100	3	10		1																				
	Fenahreh ...	100	3	9	6	5																				
	Haji Hassoun ...	100	5	10																						
	Hashimiyeh ...	100	2	2	2																					
	Hilla Town ...	100	20	11	2								2		2											
	Guss	100	3																							
	Jurf	100	7	2	2																					
	Khan Mahawil	100	10																							
	Najim Abud ...	100	21	9	8	2																				
	Tahmaziyeh ...	100	12	4	6	17																				
Kirkuk	Chemchemal ...	2,500	8	4													1									
	Kirkuk City ...	1,100	20	12																						
	Milha	700	4	4																						
Kut	Badra	250	5	1																						
	Dejeileh ...	50		2																						
	Kut Town ...	60	10	2																						
Mosul	Aradin ...	3,700	6	1																						
	Aqra	2,250	11	8		1																				
	Hamam Ali ...	600	36	57	2	3																				
	Mosul City ...	650	37	24	1																					
	Nineveh ...	650	12	10	3																					
	Qara Qosh ...	1,000	17	21																						
	Sinjar Villages	1,500	23	28																						
	Zakho Villages	1,750	25	27																						
Muntafik	Nasriyeh ...	40	16	5																						
	Suq-us-Shuyukh	30	22	12		1					2												10	1		
Pueimaniyeh	Sul. Town ...	2,750	8	2																						
	Surchinar ...	2,500	10	4																						
TOTAL			1,856	1,469	138	118	25	21	7	0	2	1	128	104	19	31	70	41	2	1	15	1	158	66	525	83


MEAN (MONTHLY) RELATIVE HUMIDITY (BAGHDAD AIRPORT)
▽ AT 0600 Hrs
+ -"- 2100 -"-
▼ -"- 1500 -"-
MEAN (MONTHLY) TEMPERATURES IN °F (BAGHDAD AIRPORT)
o MAXIMA
● MINIMA
%
°F
110
100
90
80
70
60
50
40
30
20
10
0
RELATIVE HUMIDITY.
ATMOSPHERIC TEMPERATURES.
Subgenus Phlebotomus.
o (P. papatasi only).
Subgenus Prophlebotomus
● P. sergenti, P. alexandri.
Subgenus Sergentomyia,
⊙ Group Fallax.
S. theodori var babylonica,
S. sintoni, S. dentata var
mediensis, S. mervynae.
□ Group Africana.
S. palestinensis,
S. baghdadis.
+ Group Squamipleuris.
(S. squamipleuris only).
1000
500
100
50
10
5
1
TOTAL MONTHLY CATCH.
JAN.
FEB.
MAR.
APL.
MAY
JUNE
JULY
AUG.
SEP.
OCT.
NOV.
DEC.

Lowering of the sub-soil water table in Iraq is not likely to reduce the abundance of this species, indeed it will probably be encouraged to increase by such a measure.

The distribution of sandflies of the genus *Sergentomyia* in Iraq is indicated in Map 2. Beyond the notes on each species previously given it is not proposed to discuss further their bionomics. However, it is interesting to note from the map, that, in contrast to the genus *Phlebotomus*, the individual species of the genus *Sergentomyia* are confined to one or other side of the boundary between the Saharo-Sindian and the Irano-Turanian zoo-geographical regions in this country.

The monthly prevalence of the Iraq PHLEBOTOMINAE is presented in the diagram facing. These figures must be interpreted with caution as the time spent on collecting was not necessarily the same in each month. It is considered, however, that they provide a useful guide to the relative abundance of the various groups in central Iraq. The "*fallax* group" and *S. squamipleuris* appear to have a later period of prevalence than the other types.

Climatic monthly means for Baghdad during 1950 are also presented. These figures were obtained through the courtesy of the Meteorological Officer at Baghdad airport, whose cooperation is hereby acknowledged. They were obtained from instruments in a Stevenson's screen over open, but dry, ground at the airport.

Table II gives details of the distribution of the various species of sandflies taken in Iraq. In Table III the range of these species outside Iraq is indicated, and those species recorded from neighbouring territories are included. The inclusion of exotic species in this Table and in the keys below is considered justifiable as this should assist workers unfamiliar with this subgenus who may wish to study the subject in the Middle East. Further no key for the Iraq species would be complete without the inclusion of those known to occur near the borders of the country. It is probable, for instance, that certain species at present known from Syria and Iran but not yet recorded from Iraq, will be found in this country in due course.

KEYS TO PHLEBOTOMINAE IN IRAQ AND NEIGHBOURING TERRITORIES.

Genera and Subgenera (both sexes).

1. Relatively large, pale coloured sandflies. Armature in buccal cavity absent or rudimentary. Hairs on abdominal tergites mostly erect. Prefer mammalian blood ....Genus *Phlebotomus* 2

   Usually small, often dark-coloured sandflies. Armature in buccal cavity well-developed in females, and to a variable extent in males. Hairs on abdominal tergites all recumbent or only a few erect. Prefer reptilian blood.............. Genus *Sergentomyia* 5

2. Process (peniculus) bearing a brush of hairs arising from the proximal part of the coxite. Spermatheca segmented but without terminal process............ 3

   No peniculus. Spermatheca either segmented with a terminal process, or incompletely segmented. Pharynx similar in both sexes........................ 4

3. Peniculus small with a few short hairs. Style nearly as long as coxite, and with three short terminal spines and two near the middle of the organ. Spermatheca with equal segments and an angular terminal process...Subgenus *Phlebotomus**

   Peniculus large with a brush of long hairs. Style about half the length of the coxite with two long terminal spines terminally and two long spines somewhat proximal. Terminal segment of spermatheca rounded and usually enlarged.... Subgenus *Paraphlebotomus*

4. Pharyngeal armature consisting of numerous rows of point-like teeth. Spermatheca segments with a long terminal process .... Subgenus *Larroussius*

   Pharyngeal armature consisting of a group of medium-sized teeth. Spermatheca incompletely segmented.................................Subgenus *Adlerius*

5. All abdominal hairs recumbent. Penis usually blunt but, if pointed, always associated with a definite armature in the pharynx. Spermatheca never clearly segmented... Subgenus *Sergentomyia*

   Some abdominal hairs erect. Penis sharply pointed. Pharynx without armature. About 15 teeth in the buccal cavity. Spermatheca clearly segmented......... Subgenus *Sintonius*†

* The important species, *P. papatasi*, is the only member of this subgenus found in the region.

† The only species belonging to the subgenus *Sintonius* from this region is *S. tiberiadis* Adler, Theodor & Lourie.

SUBGENUS *Paraphlebotomus*.

Males.

1. Third antennal segment longer than the epipharynx.............*jacusieli* Theodor

   Third antennal segment shorter than the epipharynx.................................2

2. Brush of hairs arising only from the tip of the peniculus............................ 3

   Brush of hairs arising not only from the tip of the peniculus but also from the ventral surface...*caucasicus* Marz.

3. Third antennal segment over 0·20 mm.....................................*sergenti* Parrot

   Third antennal segment less than 0·20 mm... 4

4. Style longer than half the coxite—about 0·125 mm..................*alexandri* Sinton

   Style about half the length of the coxite—about 0·10 mm......*maris-mortui* Theodor

Females.

(The female of *P. jacusieli* is unknown.)

1. Spermatheca with three to five segments... 2

   Spermatheca with eight to nine segments... 3

2. Pharyngeal teeth coarse and blunt, lateral ones oblique...........*caucasicus* Marz.

   Pharyngeal teeth finer, all teeth in longitudinal axis..................*sergenti* Parrot

3. Wing about 0·5 mm. ; shorter than body-length. Posterior margin of pharynx straight...*alexandri* Sinton

   Wing about same length as body. Posterior margin of pharyngeal armature concave posteriorly..*maris-mortui* Theodor

SUBGENUS *Larroussius*.

Males.

1. Penis not bifid...2

   Penis bifid...*tobbi* Adler & Theodor

2. Toothed area not extending anteriorly as far as mid-point of pharynx............3

   Toothed area extending as far as mid-point of pharynx................................ *wenyoni* Adler & Theodor

3. Penis terminates in a long, curved, blunt hook ; several minute processes near tip.......*perfiliewi* Parror

   Penis tapers to a rounded tip.......4

4. Penis very long and slender, ventral surface smooth.......
   major var. *syriacus* Adler & Theodor

   Penis tapering, of moderate length, lower margin serrated... ....
   kandelakii Shurenkova

Females.

1. Toothed area of pharynx not extending beyond posterior third.......2
   Toothed area extending beyond posterior third.......4

2. Spermatheca with 30–35 segments, posterior ones not clearly defined.......
   kandelakii Shurenkova

   Spermatheca with about 15 clearly definable segments.......3

3. Rather dark colour. Length 2·4–3·0 mm. Pharynx similar to that of *P. perniciosus*—numerous rows of fine pointed teeth ; the rows having a marked convexity posteriorly. Posterior border of toothed area also convex.......
   tobbi Adler & Theodor

   Paler in colour. Length about 2·0 mm. Pharyngeal teeth larger and arranged more openly ; the rows of teeth hardly convex posteriorly......*perfiliewi* Parrot

4. Toothed area of pharynx extending anteriorly at least to the mid-point of the pharynx.......*wenyoni* Adler & Theodor

   Toothed area not extending to the mid-point of pharynx.......
   major var. *syriacus* Adler & Theodor

SUBGENUS *Adlerius.*

Males.

1. Penis pointed with preterminal tubercle or notch.......2
   Penis with rounded tip.......*larroussei* var. *canaaniticus* Adler & Theodor

2. Genital filaments about 13 times the length of the pump. Penis with preterminal notch.......*chinensis* var. (near *longiductus* Parrot)

   Genital filaments about 7 times the length of the pump. Wedge-shaped preterminal tubercle on penis.......*chinensis* var. *simici* Nitzul.

Females.

1. Spermatheca spindle-shaped 2
   Spermatheca tubular.......*larroussei* var. *canaaniticus* Adler & Theodor

2. Toothed area in pharynx extending only to one-fifth of the long axis, teeth darker in colour than in other races. Size 1·6–1·8 mm.......
   chinensis var. *simici* Nitzul.

   Toothed area in pharynx occupying posterior one-third of the organ. Size 2·6–3·2 mm.......*chinensis* var. (near *longiductus* Parrot)

SUBGENUS *Sergentomyia.*

Males.

1. Buccal armature consisting of not less than 30 easily definable parallel teeth......2
   Buccal armature with less than 30, usually weakly chitinised teeth.......3

2. Dark coloured sandfly. Wall of the buccal cavity thickened in such a way as to produce a bilateral projection just anterior to the armature. Coxite less than 0·2 mm. in length. Paramere short and clubbed........................ *squamipleuris* (Newst.)

   No thickening in the wall of the buccal cavity. Coxite more than 0·2 mm. in length. Paramere hooked........................*africana* var. *asiatica* (Theodor)

3. Paramere hooked at the tip..4

   Paramere blunt at the tip or clubbed..6

4. Paramere without a ventral spine-bearing process......................................5

   Paramere with a process arising near its base, from which a group of stout spines originate..*hodgsoni* (Sinton)

5. Buccal armature consists of about six blunt, weak, spines arising on a very shallow arc. Ascoids (geniculate spines) on antennal seg. III. very short—less than one-twentieth of the length of the segment. Pharyngeal armature consists of about six transverse rows of minute teeth (fig. 9).................... *palestinensis* (Adler & Theodor)

   Buccal teeth usually almost indistinguishable and standing on a deep arc. Pharynx without chitinous teeth. Ascoids on antennal segment III. about one-tenth of the length of the segment..............*baghdadis* (Adler & Theodor)

6. All spines on style arising terminally..7

   Some spines arising sub-terminally...9

7. Seta arising proximally to the roots of the spines, about one-fifth of the distance from the distal extremity of the style.....................................8

   Seta may be difficult to distinguish, always weakly developed ; arising near the the roots of the terminal spines. About 12 buccal teeth. Style over five times as long as broad..*fallax* (Parrot)

8. Buccal cavity with about 25 teeth on a shallow arc; the medial teeth are relatively small...*theodori* (Parrot)

   About 14–18 indistinct teeth in the buccal cavity, on a shallow arc. Little gradation between the medial and lateral teeth (figs. 1 & 2) .... *theodori babylonica*, **var. n.**

9. Two spines arising sub-terminally..10

   The tubercle of one spine produced, giving the impression of three spines arising sub-terminally (fig. 8). About 16 regularly spaced buccal teeth on a shallow arc (fig. 7)..*mervynae*, **sp. n.**

10. Buccal cavity contains 10–14 evenly spaced teeth (fig. 3). Coxite from 0·20-0·23 mm. in length. Seta arises near the base of the sub-terminal pair of spines. Penis slender (fig. 4)...*sintoni*, **sp. n.**

    About 20 teeth in the buccal armature, the medial teeth are relatively small and closely set. Coxite from 0·25–0·27 mm. in length. Seta arises proximally to the bases of the sub-terminal spines (figs. 5 & 6)......*dentata mediensis*, **var. n.**

Females.

1. Spermatheca tubular and weakly chitinised..2

   Spermatheca capsular and strongly chitinised...9

   Spermatheca turnip-shaped and decorated with transverse rows of minute brown spines. About 50 parallel teeth in the buccal cavity. Marked lateral buccal protuberance..*squamipleuris* (Newst.)

2. Spermatheca unmarked..3

Spermatheca marked by a delicate, more or less transverse tracery of fine lines, irregularly reticular. About 30 parallel teeth on a shallow arc in the buccal cavity. Pigmented area large, reddish-brown, and tapering forwards in the mid-line..*hodgsoni* (Sinton)

3. Buccal teeth graded from well-developed lateral teeth to smaller, more closely set medial teeth...4

Buccal teeth fairly uniform in size or spacing..7

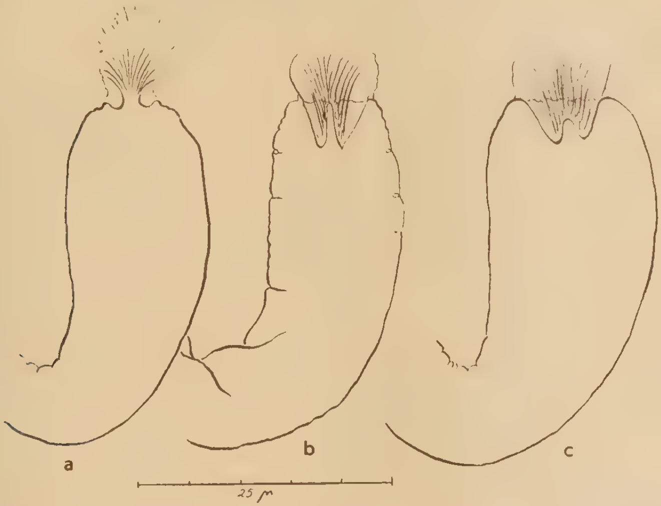


Fig. 10.—Spermathecae of (*a*) *S. mervynae*; (*b*) *S. theodori* var. *babylonica* (empty); (*c*) *S. theodori* var. *babylonica* (normal).

4. Pharynx deeply indented posteriorly...5

Posterior margin of pharynx almost straight...6

5. Length of pharynx less than twice its greatest width. Buccal cavity with 14–20 teeth (fig. 1). Pigment, when present, limited to a transverse oval overlying the centre of the buccal armature..........................*theodori babylonica*, **var. n.**

Pharynx about twice as long as broad, often more so. About 24–28 buccal teeth. Pigmented area apparently variable but usually in the form of a rounded triangle with the apex extending anteriorly to the edge of the buccal plate... *theodori* (Parrot)

6. About 20 spinous teeth in the buccal cavity (fig. 5). Pigmented area shaped like the segment of an orange. Pharynx (fig. 5) with a strong armature of blunt teeth, the posterior rows of which are discrete. Spermathecal duct almost as wide as the terminal bulb, which is deeply umbilicated (fig. 11).................. *dentata mediensis*, **var. n.**

About 16 buccal teeth (fig. 7). Pigmented area tapers as it extends forwards of the buccal plate. Pharynx (fig. 7) with a group of deeply chitinised blunt teeth in the anterior portion of the armature, the posterior part of which is only weakly chitinised. Spermatheca (fig. 10) without obvious umbilication......... *mervynae*, **sp. n.**

7. Posterior margin of pharynx not indented...8

Posterior margin of pharynx indented. About 17 buccal teeth, the medial five of which are somewhat shorter than the lateral teeth but are as widely spaced. Pigmented area rounded..*fallax* (Parrot)

TABLE III.

Distribution of the Sandflies of Iraq and neighbouring Territories, by Countries.

	Species	Iraq	Jordan	Israel	Iran	Syria	Lebanon
Phlebotomus Subgenus *Phlebotomus*	1. *P. papatasi* (A, P)	×	×	×	×	×	×
Subgenus *Paraphlebotomus*	2. *P. sergenti* (A, P)	×	—	×	×	×	×
	3. *P. alexandri* (A, P)	×	—	×	—	—	—
	4. *P. caucasicus*	—	—	—	×	—	—
	5. *P. jacusieli*	—	—	×	—	—	—
	6. *P. maris-mortui*	—	—	×	—	—	—
Subgenus *Larroussius*	7. *P. kandelakii*	—	—	—	×	—	×
	8. *P. major* (P)	—	×	—	—	—	×
	9. *P. major* var. *syriacus*	—	—	×	—	×	—
	10. *P. perfiliewi*	—	—	×	—	—	—
	11. *P. tobbi*	—	—	×	×	—	—
	12. *P. wenyoni*	×	—	—	×	—	—
Subgenus *Adlerius*	13. *P. chinensis* var. *simici*	—	—	×	×	—	—
	14. *P. chinensis* var. (near *longiductus*) (P-var.)	—	—	—	×	×	—
	15. *P. larroussei* var. *canaaniticus*	—	—	×	—	—	—
Sergentomyia Subgenus *Sergentomyia* Group *minuta*	16. *S. hodgsoni* (P)	×	—	—	—	—	—
Group *fallax*	17. *S. fallax* (A-var.)	—	—	×	—	—	—
	18. *S. theodori*	—	—	×	—	×	×
	19. *S. theodori* var. *babylonica*	×	×	×	—	—	—
	20. *S. dentata* var. *mediensis* (P-var.)	×	—	—	—	—	—
	21. *S. sintoni* (P)	×	—	—	—	—	—
	22. *S. mervynae*	×	—	—	—	—	—
Group *africana*	23. *S. africana* var. *asiatica* (A-var.)	—	—	×	—	—	—
	24. *S. baghdadis* (P)	×	—	—	—	—	—
	25. *S. palestinensis*	×	—	×	×	—	—
Group *squamipleuris*	26. *S. squamipleuris* (A) (P-var.)	×	—	—	—	—	—
Subgenus *Sintonius*	27. *S. tiberiadis*	—	—	×	—	—	—

Note : " (A) " after the name of the species indicates that it has been recorded from Africa. The letter " (P) " indicates that it is known to occur in Pakistan. " (A-var.) " and " (P-var.) " indicate that closely related forms occur in Africa and Pakistan, respectively.

8. About 12 teeth in buccal cavity (fig. 3); pigmented area broadly triangular. Pharynx (fig. 3) with armature of large, blunt teeth, deeply pigmented throughout. Spermatheca with umbilication (fig. 11)............*sintoni*, **sp. n.**

About 16 teeth in buccal cavity (fig. 7). Pigmented area tapers in the mid-line anteriorly. Pharynx with a group of deeply chitinised blunt teeth in the anterior portion of the armature (fig. 7), the posterior part of the armature is only weakly chitinised and slightly armed. Spermatheca (fig. 10) without obvious umbilication..*mervynae*, **sp. n.**

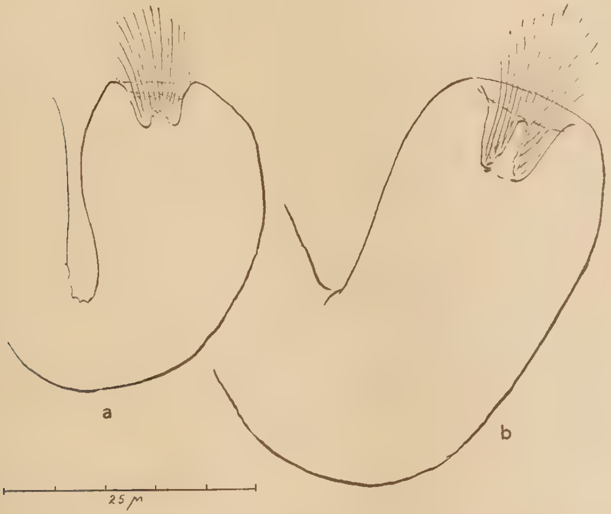


Fig. 11.—Spermathecae of (*a*) *S. sintoni*; (*b*) *S. dentata* var. *mediensis.*

9. Spermatheca about twice as long as broad..10

Spermatheca rounded with a proportion of length to breadth of 4 : 3. Buccal armature with about twenty parallel teeth on a straight line. The pigmented area is often heart-shaped and the anterior tail is often bifid.................... *palestinensis* (Adler & Theodor)

10. Capsule of spermatheca heavily chitinised throughout; duct narrow. Buccal armature consisting of 40–50 teeth with a triangular pigmented area............ *africana* var. *asiatica* (Theodor)

Capsule of spermatheca heavily chitinised only in distal two-thirds; duct wide. Buccal armature consisting of 16–18 teeth on a deep arc, just posterior to a notch in the margin of the buccal plate............*baghdadis* (Adler & Theodor)

Summary.

An account is given of a survey of the sandfly fauna of Iraq made in 1949 and 1950. Two new species, one of which has been previously misidentified, and two new varieties are described, and brief notes are given on all the 12 species of *Phlebotomus* and *Sergentomyia* taken in the survey. A description is given of a male of *P. palestinensis* taken in Baghdad, as it differs from the male described from Jericho. Keys to the Phlebotominae in Iraq and neighbouring territories are included, together with a Table showing their distribution.

Relationship between distribution of human dermal leishmaniasis and the species of *Phlebotomus* is shown on a map, supporting the belief that *P. sergenti* is the principal, if not the sole, vector of oriental sore in Iraq.

The distribution of *Sergentomyia* is given in another map indicating that, in contrast to *Phlebotomus*, the individual species of *Sergentomyia* are confined to one or other side of the boundary between the Saharo-Sindian and the Irano-Turanian zoo-geographical regions.

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